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Seasonality and Predictability: The Hormonal and Behavioral Responses of the Red-Bellied Lemur, *Eulemur rubriventer,* in Southeastern Madagascar

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Seasonality and Predictability: The hormonal and behavioral responses of the red-bellied lemur, *Eulemur rubriventer,* in Southeastern Madagascar

by

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Dedication

To Sleeper for his patience, understanding, and flexibility.

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Seasonality and Predictability: The hormonal and behavioral responses of the red-bellied lemur, *Eulemur rubriventer,* in Southeastern Madagascar

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This dissertation investigates the relationship between Madagascar's environment and the stress physiology of the red-bellied lemur, *Eulemur rubriventer*. Unique lemurid traits are proposed to have evolved in response to selection pressures unlike those in other primate habitats, and appear to be particularly suited to helping animals cope with harsh and unpredictable environments. Several hypotheses as to why lemurs evolved characteristics such as small group sizes, low basal metabolic rates, and cathemerality rest upon the untested assumption that these species are ecologically and/or reproductively stressed.

This study simultaneously analyzes seasonal changes in climate, ecology, and the behavior and stress hormones (cortisol) of *Eulemur rubriventer,* as well as differences in these parameters across habitats with different ecological matrices. The goals of this dissertation are to: (1) evaluate the influences of seasonally varying food availability and

climate upon lemur behavior and physiology, to determine whether such changes are sufficient to exert strong selective pressure; and (2) assess the additional influences of habitat composition and quality to evaluate the effects of unpredictability and habitat disturbance.

Eulemur rubriventer are sensitive to seasonal environmental changes, as indicated by their time budgets, diets, and fecal cortisol levels. Overall they adopt a time minimizing strategy whereby energy is conserved by resting a majority of the time. Ripe fruit scarcity periods elicit the launch of an energy maximizing strategy whereby fecal cortisol levels and time feeding increase, and time resting decreases. Sensitivity to these influences varies across habitats. The behavioral and stress responses of groups in the undisturbed habitat (UND) were more seasonal and pronounced than those from their disturbed habitat (DIST) counterparts. Lower cortisol levels in DIST may result from a less seasonally predictable environment requiring frequent short-term responses (with possible energy deficits during critical reproductive stages yielding 3 deaths out of 5 births and out-of-season reproduction). Alternatively, the attenuated behavioral and hormonal response to environmental change in DIST may indicate a severely stressed population with insufficient energy to launch an appropriate coping response. The hypothesis that animals in DIST have adapted to frequent unpredictability due to disturbance is rejected because all animals behaviorally and hormonally respond to fruit declines, indicating that this species undergoes ecological stress.

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Chapter 1: Introduction

BACKGROUND

Living in Dynamic Environments

Life history theory predicts that reproduction and growth schedules are the result of adaptation to the limitations of a particular environment (Charnov, 1993), and these schedules afford animals the greatest likelihood of survival and reproduction in such an environment (Daan and Tinbergen, 1997). In maximizing fitness, animals are often faced with the challenge of living in a varying environment. Even the most static environments are subject to change (Terborgh, 1986a; Negus and Berger, 1987) and present animals with spatially and temporally varying accessibility to food as well as changes in the thermal environment. Although tropical environments were viewed in the past as relatively unvarying (Wikelski *et al.,* 2000), we now know that many are characterized by seasonal environmental changes (Terborgh, 1986a; van Schaik and Pfannes, 2005). As a result, tropical species experience varying energetic requirements and varying challenges to meeting those requirements (McNab, 1980). Working within the confines of dynamic environments to survive and successfully reproduce, these species are forced to enter a resource allocation trade-off. For instance, the processes of maintenance, foraging, and thermoregulation are of primary importance for most species (Bronson, 1995). As the demands of one of these processes increase, energy devoted to others must decrease to remain energetically balanced, or secondarily important processes such as growth and

reproduction will be sacrificed (Bronson, 1989). For example, if an environment is too poor to energetically support a reproducing female during early pregnancy, the embryo may be aborted (Bronson, 1995). Smits and colleagues (1998) found a seasonal pattern to effective fecundability in humans, and Weinberg and colleagues (1994) found a seasonal influence on spontaneous abortion, indicating some environmental influence upon the ability of a woman to effectively reproduce. Avoiding energy declines is thus extremely important for fitness because the energetic trade-off may result in the sacrifice of reproductive ability.

The predictability of an environment can have profound implications upon the strategy by which species maintain energetic homeostasis. Highly seasonal environments may be characterized by severe seasonal disparities in food supply. Although these environments may be seasonally predictable, species may still undergo periods of energetic challenge during food shortages and experience decreased body condition (Knott, 1998; Wikelski *et al.,* 2000; Lewis and Kappeler, 2005). If periods of food availability and scarcity can be predicted from year to year, however, animals can adjust their activity levels and schedule reproduction appropriately to avoid severe energy decline and maximize fitness. Many species in these environments utilize cyclical, predictable environmental cues to precisely time reproduction (Negus and Berger, 1972). Species in highly seasonal environments are often tightly entrained to photoperiodic (pertaining to the ratio of daylight to darkness) cues, and reproduction often occurs in tight synchrony within populations as all individuals exploit the predictability of the environment for optimal reproduction (Negus and Berger, 1972; Wikelski *et al.,* 2000). In fact, Spotted Antbirds in the Neotropics anticipated seasonal changes to such a degree

that gonadal increase in all males occurred approximately 1.5 – 2 months prior to the wet season (Wikelski *et al.,* 2000).

Some seasonal environments may be inter-annually unpredictable, however, and require more flexibility on the part of animals to gain sufficient nutrients from the environment. van Schaik and Pfannes (2005) report that areas subject to frequent hurricanes/cyclones (many tropical habitats) have great inter-annual rainfall variability, and some areas in southeast Asia (variously seasonal) experience intense inter-annual fruiting variability (masting) (see also van Schaik and van Noordwijk, 1985). Since rainfall and food availability are not as predictable as photoperiod, even in largely predictable regions, scheduling activities with photoperiod may not be the most optimal strategy in terms of maintaining sufficient energy levels, and additional short-term cues may be used in these habitats. For instance, while Spotted Antbirds in the Neotropics time reproduction by using long-term cues such as seasonal photoperiod, they additionally modify behavior in response to rainfall and food availability (Wikelski *et al.,* 2000). Other species such as Microtine rodents (*e.g.,* voles) who feed primarily upon Monocots in unpredictable environments may respond to a compound (6-MBOA) found in the young shoots of their low quality food sources (Berger *et al.,* 1981). Since the relationship between photoperiod and food availability is not predictable, these species use the presence of 6-MBOA as an honest cue to predict food availability and initiate breeding (Berger *et al.,* 1981; see Negus and Berger, 1987 and Nelson *et al.,* 2002). Thus, short-term cues may be superimposed upon long-term cues to help species determine optimal strategies for energy allocation and reproduction (Wingfield, 2005).

The main challenge for animals in acquiring and ingesting food is balancing energy expenditure with energy intake. To acquire sufficient nutrients and ensure that the

energy spent searching for food will be replenished, animals may depend upon the level of resource predictability, selecting certain behavioral and dietary strategies based upon what food is available, where it is available, and when it is available. For instance, ecologists often label certain times of the year 'lean seasons' because, although food may be available, it may be more distantly or sparsely located or poorer in nutritional quality than during other times of the year. To accommodate the challenges inherent in acquiring distantly located and/or poor-quality foods, and avoid the detrimental effects of stress, species must store energy prior to the lean season (*e.g.,* Knott, 1998), and/or shift activity (or ranges) during the lean season.

Seasonality and Behavioral Flexibility

Behavioral modifications to accommodate changing energetic needs can vary greatly among animals, even closely related species. The ways in which species vary their daily and seasonal time budgets can provide a detailed assessment of energetic strategies due to the plastic nature of behavior (Coelho, 1986; Vasey, 2005). In particular, mammals appear able to adjust time spent feeding, resting, and traveling in an energetic (and risk) trade-off (Cuthill and Houston, 1997; Nash, 1998; Halle and Stenseth, 2000). Optimal Foraging Theory (MacArthur and Pianka, 1966; Stephens and Krebs, 1986; Krebs and Davies, 1997) predicts that feeding and traveling change relative to one another, and that an activity can occur to the extent that the time spent per unit energy gained exceeds the loss (MacArthur and Pianka, 1966). To minimize energy expenditure, animals may spend more time resting by spending less time feeding or traveling, settling for foods nearby when rare, high quality resources do not exist (Schoener, 1971; Cuthill and Houston, 1997); to maximize energy, animals may spend more time feeding and traveling (and less time resting) to find quality food from diverse

resources. Many animals including primates (Overdorff *et al.*, 1999; Boinski *et al.,* 2005), birds (Morton, 1977; Keuroghlian, 2003), bats (Richter and Cumming, 2006), and ungulates (Carrillo *et al.,* 2002) may even migrate to remote areas which are higher in food abundance, and establish entirely new home ranges for the duration of the lean season (Hemingway and Bynum, 2005). These strategies are impacted by factors such as the quality and digestibility of available food, the thermal environment, and reproductive condition. For instance, species employing an energy maximizing strategy may increase feeding time by consuming either (A) poorer quality, less digestible foods for longer periods of time or (B) a large diversity of rare, patchy, high quality foods to accomplish adequate energy intake (MacArthur and Pianka, 1966; Schoener, 1971; Clutton-Brock and Harvey, 1977; Dunbar, 1988; Overdorff, 1988; Passamini, 1998).

Shifting diets seasonally (diet switching) may occur by feeding upon different, or more or less diverse, plant species or plant parts (Hemingway and Bynum, 2005). In an extensive comparative study of dietary flexibility in 119 primate species, Hemingway and Bynum (2005) found that dietary breadth (shifting plant species) and dietary variability (shifting plant parts) were inversely related, and suggest that as primates feed upon more plant species, the need to feed upon different plant parts is alleviated. However, these dietary patterns are not mutually exclusive, and interspecific differences due to gut morphology, among other traits, will also influence a species' behavior.

Investigating seasonal fluctuations in the amount of time devoted to feeding, traveling, resting, and social behaviors informs on how species meet myriad challenges, including changing climate and food availability, since they are related to energy intake, conservation, and expenditure. Furthermore, determining the manner of behavioral flexibility employed by species in response to seasonal changes can indicate how they

might respond to natural or anthropogenic habitat alterations, an increasingly relevant topic in wildlife studies. Adaptations to such dynamic environments are likely reflected in reproductive fitness strategies.

Seasonal Breeding, Seasonal Environments, and Selection

Breeding most often occurs seasonally (for reviews see Lancaster & Lee, 1965, van Horn & Eaton, 1979, Lindburg, 1987; Brockman & van Schaik, 2005; Janson & Verdolin, 2005), yet this is not always the case. Some species reproduce aseasonally, with no apparent pattern, and are *seemingly* not greatly reproductively affected by periods of relatively lower food availability or do not experience fluctuations in food availability at all. When living with humans, in contrast to environments where resource availability fluctuates greatly, the house mouse reproduces aseasonally (Berry & Bronson, 1992) because energy balance may be maintained at sufficient levels for reproduction any time of the year regardless of the minor fluctuations in food availability that might occur. However, maintaining such a high energetic condition is extremely rare, even in human populations (Ellison *et al.,* 2005). More often, aseasonal breeding occurs because environmental fluctuations, be they seasonal or not, can not be predicted and necessitate the relaxation of seasonal reproduction if infants are to survive. Both seasonal and aseasonal breeders may exist in seasonal or aseasonal environments; which strategy is employed depends more upon the predictability of the environment.

When the environment is unpredictable and species can not anticipate when or where food might be abundant, breeding seasonality may occur or it may be relaxed. The extent of this flexibility in reproductive timing depends upon the energetic condition of the female; energetic stress can suppress reproduction to conserve reproductive effort when the environment is unfavorable, and natural selection acts on the breeding female

(Brockman and van Schaik, 2005). This may occur through two-way hormone/behavior interactions in which environmental conditions affect hormones such as progestin (P_4). Even in species which may reproduce year-round *(e.g., Papio cynocephalus)*, when environments are harsh the P_4 threshold for successful implantation may rise such that higher levels of P_4 are required than during other times of the year (Wasser, 1996). These highly opportunistic breeders (May and Rubenstein, 1985) adopt a facultative reproductive strategy (Negus and Berger 1972) and have been termed alternative breeders (*primates* van Schaik and van Noordwijk, 1985) and/or capital breeders (*birds* Drent and Daan, 1980; *plants and animals* Jönsson, 1997) because they may take advantage of food abundant periods by storing nutrients (Richard *et al.,* 2000), and breed once they reach high enough stores for successful reproduction (hereafter these species will be referred to as *opportunistic*). Changes in the population sizes of opportunistic species are due to differential reproductive performance (Negus and Berger, 1972).

In highly seasonal and predictable environments many species rely upon predictive cues about the future and seasonal breeding is more common (Negus and Berger, 1972). Rather than relying upon environmental productivity and energetic state in the immediate sense, selection has acted on the timing of reproductive activities so that animals use environmental cues such as photoperiod (Sadleir, 1972), regardless of the current state of the energetic environment. For instance, the most expensive time for many female species is late-lactation and early weaning (Jolly, 1984; Coelho, 1986; Bronson and Heideman, 1994) and several taxa (*e.g.,* birds, primates, bovids) time this activity with the time of year most likely to be abundant with food (Lack, 1950; Altmann, 1980; van Schaik and van Noordwijk, 1985; Bronson, 1995; Wright, 1999; Di Bitetti and Janson, 2000; Lewis and Kappeler, 2005). This way they are able to maintain energetic

balance and infants have the advantage of independent foraging with plenty of food available. The strategy of completing weaning before food declines may also result in lower mortality rates for newly independent offspring (Pereira, 1993; Bronson and Heideman, 1994). If infant independence coincides with the lean season, infant mortality would likely rise; in Alaska, moose born later in the year die earlier in the first year of life (Keech *et al.*, 2000), so there is probably strong selective pressure exerted at this time (Brockman and van Schaik, 2005). In contrast with opportunistic breeders, changes in the population sizes of these species are due to differential mortality (Negus and Berger, 1972).

For species to know when to *breed*, however, they must rely upon cues that are reliably predictive about the future rather than indicative of the current state of the environment. Reliance upon predictive cues is particularly important in species which conceive and give birth in different seasons (Wright, 1999). For instance, breeding in white-tailed deer occurs during the fall when deer energy levels are waning, and is cued by daylength (see Bronson, 1995). Conception in many lemurid species must also occur during the lean season in order to time late lactation and weaning with food abundance (Wright, 1999). These species are tightly entrained to photoperiod (Rasmussen, 1985; Bronson, 1995) so that they may initiate reproduction when not in energetically prime condition. In fact, this entrainment is so strong in several species (e.g. tammar wallabies and lemurs) that animals continue to breed seasonally when in captivity and provisioned. The time differential between wild and captive reproductive events occurs in lock-step with the latitudinal differential (Rasmussen, 1985; Negus and Berger, 1987). This strategy has been termed predictive cuing (May and Rubenstein, 1985) or obligate reproduction (Negus and Berger, 1972). Animals who employ this strategy have been

termed income breeders (*birds* Drent and Daan, 1980) and/or classic breeders (*primates* van Schaik and van Noordwijk, 1985), since they must rely upon what energy is available in the environment at the time (hereafter these species will be referred to as *obligate*). Selection for reproductive *timing* through seasonality probably secondarily selected for reproductive *synchrony* (Post, 2003), where population birth peaks ("the period of the year in which a high proportion of births but not all births are concentrated" Lancaster and Lee, 1965, p. 488) occur.

The reality in nature is actually less clear-cut than the perceived (and modeled) dichotomy between opportunistic and obligate breeders. On the one hand, endogenously cued opportunistic breeders depend upon energy reserves to determine when they breed. On the other hand, exogenously cued obligate breeders can breed without maintaining high energy levels. But it might be expected that, in unusually productive years with abundant available energy (i.e., food), strict obligate breeders entrained to photoperiod might be more flexible in when they breed. Negus and Berger (1972) did suggest that most mammalian species are actually somewhere between the opportunistic and obligate breeders. The house mouse may be a prime example. When living in environments where food is seasonally available there is strong seasonality of reproduction, in contrast with house mice living in human houses (Berry and Bronson, 1992). Relaxation of strict seasonal breeding only occurs when food is constantly available. In fact, Brockman and van Schaik (2005) and Janson and Verdolin (2005) both suggest that relaxed seasonal breeding is a strategy in and of itself; they propose a third category whereby animals are entrained to photoperiod or other seasonal cues, yet subject to relaxation of strictly timed seasonal breeding through increased food availability. These so-called 'relaxed income' (Brockman and van Schaik, 2005) and 'income II' (Janson and Verdolin, 2005) breeders

are seasonal and rely upon predictive cues, timing late-lactation and weaning with food abundance, yet the ability to conceive depends upon the female's energetic condition (or more broadly, as in the case of Spotted Antbirds, rainfall and food availability, Wikelski *et al.*, 2000). The result is a wider birth peak and prenatal and postnatal mortality rates between that predicted for the other two strategies (Brockman and van Schaik, 2005), which is what would be expected with relaxed selection on either end of the reproductive cycle. Wider birth peaks should be expected to a certain extent if balancing selection were occurring in response to inter-annual variation in food abundance (Daan and Tinbergen, 1997). Therefore, the condition of the environment, and thus the energetic condition of the reproductive female, may affect reproductive success at the conceptive, prenatal, and late-lactation/ablactating stages in species adopting such a strategy.

The implications of these strategies upon the timing of life history events are great. While numerous studies have assessed the effects of seasonality and food scarcity on the timing of life history variables (*e.g.,* Richard *et al.,* 2002; Pochron *et al.,* 2004), there is a paucity of data that *directly* address the relationship between food availability and the stress experienced by a species. At the most basic level, it has not been widely tested whether wild species experience energetic stress when food is scarce (but see Knott 1998, Strier *et al.* 1999, Cavigelli 1999, and Chapman *et al.* 2006). Determining whether food scarcity has the potential to exert selective influence upon species is essential in understanding their particular suite of life history traits, and must first be addressed by assessing what energy exists in the environment and how animals accumulate, store, and expend that energy. We can then begin to understand how animals resolve the "competing needs for optimizing survivorship and reproductive effort" (Bribiescas, 2001, p. 148). Studies concurrently examining and quantifying all of

these factors in detail are rare. To address this gap in current knowledge, this study measures the relationships between climate, habitat productivity, behavioral flexibility, and energy levels in a seasonally breeding lemur species to determine (1) *whether* a seasonally breeding species experiences energetic stress; (2) *when* energetic stress occurs in relation to the state of the environment; and (3) *how* a seasonally breeding species behaviorally copes with and mitigates energetic stress.

Physiological Stress

Selye (1950) first postulated that the vertebrate stress response helps the body achieve homeostasis and is nonspecific: glucocorticoids are secreted in response to many different types of stressors. In other words, a physiological, environmental, or psychosocial stressor will all produce the same response within the vertebrate endocrine system. Further research suggests that the stress response is more specific than Selye (1950) suggested and depends upon how stress is perceived by the organism. For instance, the body experiences and overcomes gradual stress such as seasonal temperature changes by slight physiological changes which *maintain* homeostasis. However, sudden or unpredictable stressors such as a predation event initiate a response which helps *reestablish* homeostasis (Sapolsky, 1994; Chrousos *et al.*, 1998; Nelson and Klein, 1999; see Selye, 1980; for views on the utility of the stress concept and the replacement of 'stress response' with 'allostatic response', see Sterling and Eyer, 1988; Dallman, 2003, McEwen and Wingfield, 2003ab, Schulkin, 2003, Walsberg, 2003). This type of response may be initiated by both natural disturbances (such as environmental change, predation, and social instability), and anthropogenic disturbances (such as noise and habitat alteration).

The perception of a stressor initiates a suite of behavioral and physiological responses including the release of glucocorticoids in the hypothalamic-pituitary-adrenal (HPA) axis (Figure 1.1). The stress response is an extremely extensive and intricate process involving the immune, endocrine, and central nervous systems, and has been reviewed in detail by Chrousos (1998). One aspect of the stress response involves the organs of the HPA axis, which are stimulated to secrete chemical messengers (*e.g.,* hormones and neurotransmitters) which stimulate and regulate other chemical messengers and are capable of suppressing certain physiological functions deemed unnecessary during the stress response. A negative feedback loop down-regulates itself as the stressor subsides and the body copes. During this process glucocorticoids such as cortisol are secreted by the adrenal cortex to help ensure that adequate energy is available to meet increased metabolic demands, in proportion to the stressor's intensity (Figure 1.1) (Hennessy *et al.,* 1979). Essentially all vertebrates have evolved physiological coping adaptations which allow them to respond to energetically demanding (stressful) conditions.

Stress and Darwinian Fitness

Both acute and chronic stressors affect the HPA axis and the interaction between hormones and behavior. Although the term 'stress' carries negative connotations, the stress response evolved because it is adaptive. For instance, acute stress responses help organisms mobilize energy in emergency situations. Energy is temporarily redirected away from long-term survival functions (Sapolsky, 1987) which are deemed unnecessary during the stress response, such as reproduction (Coe *et al.,* 1982; Sapolsky, 1985; Wingfield *et al.,* 1997), territorial behavior (Wingfield *et al.,* 1997), and immune function (Cohen, 1988; Khansari *et al.,* 1990; Dobbin *et al.,* 1991), and toward the immediate

needs of the organism (Chrousos, 1998). When exposed to an acute stressor, the cost of temporary inhibition of these long-term functions is generally outweighed by the benefit of energy mobilization, and ultimately this response may increase reproductive success by helping the individual through an emergency such as a predation event (Lee and Cockburn, 1985) and avoiding chronic stress (Breuner *et al.*, 1999).

However, the actions of glucocorticoids may become maladaptive when individuals are subject to chronic (weeks or months) stressors (Selye, 1956; Coe and Scheffler, 1989; Sapolsky, 1994). When mammals undergo a negative energy balance, reproductive function is impaired (Bronson, 1999). *Prolonged* stress suppresses reproduction to the point that it may cause impotence, anovulation, and loss of libido (Sapolsky, 1992). While rises in the glucocorticoid cortisol during reproductive periods may co-occur with increased fertility (Bercovitch and Ziegler, 2002), cortisol secretion associated with reproduction may increase to higher levels in response to induced stress (Saltzman *et al.,* 1994), and cortisol has been found to inhibit female primates' ability to reproduce (Wasser and Starling, 1988; Mendoza and Mason, 1988; Chatterton *et al.,* 1991; Sapolsky, 1992; Cameron, 1997; Bronson, 1999). Physiological modifications in response to stress during reproductive stages can be particularly detrimental to reproductive success in slowly reproducing species such as primates. Prolonged stress may also inhibit immune function and affect susceptibility to parasite infestation and disease (Esch *et al.,* 1975; Keller *et al.,* 1983; Laudenslager *et al.,* 1983; Cohen, 1988; Chapman *et al.*, 2006; Muehlenbein, 2006), which can in turn increase energy expenditure, decrease digestion, and reduce reproductive output (Coop and Holmes, 1996).

Due to its effects on longevity and reproduction, the study of stress has wide-ranging implications for reproductive success. Extended activation of the HPA axis is likely to result in detrimental fitness consequences in a wide range of vertebrate species [*reproductive failure*: Sapolsky, 1985 (primates), Arnold and Dittami, 1997 (marmots),; *abandonment of offspring, reduced survival of young, increased mortality*: Colwell *et al.,* 1988, Negus and Berger, 1987, Cotter and Gratto, 1995, Rodway *et al.,* 1996 (birds); *decline in longevity*: Burrows *et al.,* 1994 (wild dogs)]. Hormonal analyses are a promising avenue of research to better assess the relationship between stress and reproductive success in vertebrate species.

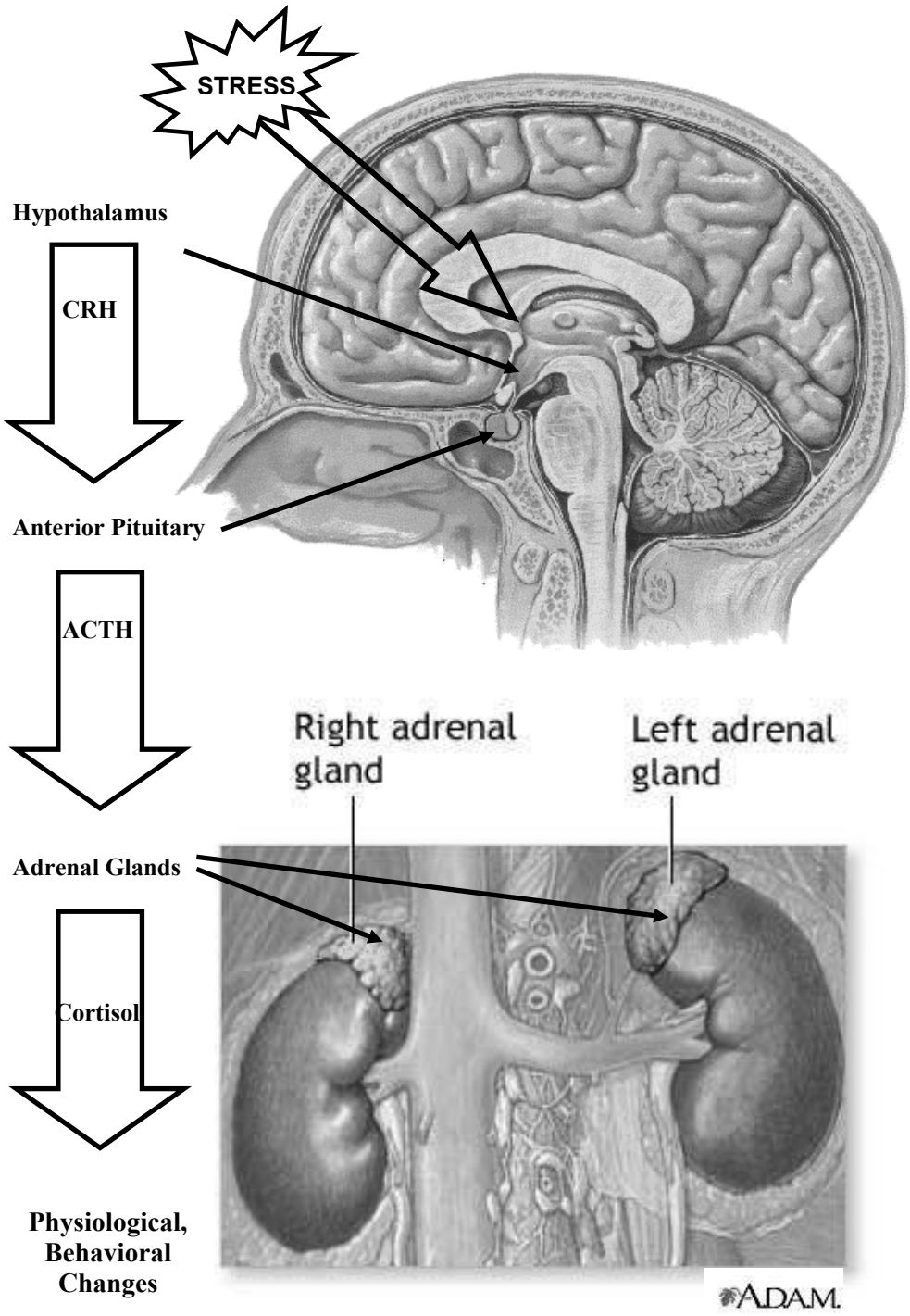


Figure 1.1. Hypothalamic-Pituitary-Adrenal Axis and the Stress Response. When a stressor is perceived the hypothalamus is stimulated to secrete corticotropin releasing hormone (CRH) which stimulates the anterior pituitary to secrete adrenocorticotropic hormone (ACTH). ACTH stimulates the adrenal cortex on the kidneys to secrete glucocorticoids such as cortisol. This initiates a cascade of physiological and behavioral adjustments. Brain image from Furman.edu; Adrenal image from A.D.A.M., Inc.

Measuring Stress: Cortisol

While a number of indicators have been used to assess stress levels, glucocorticoids such as cortisol and corticosterone are, as a group, currently considered one of the most reliable and widely applied measures. For instance, though heart rate is a dependable indicator of metabolic rate, it may not always reflect a stress response (Harlow *et al.,* 1987; Hofer and East, 1998). Behavioral data, too, were found to be less sensitive than cortisol measures in recording psychosocial stress events in several studies of vertebrate taxa (Coe *et al.,* 1982; Paterson and Pearce, 1992; Schapiro *et al.,* 1993; Clarke *et al.,* 1996; Gust *et al.,* 1996; Smith and French, 1997; but see Mendoza and Mason, 1988). Population density has also been used as a measure of stress (Glessner and Britt, 2005) with low population density indicating a stressful environment. However, population density alone is not a good indicator of stress because populations often remain high when habitats shrink or decline in quality (Hofer and East, 1998). Catecholamines (adrenaline, dopamine) may be the most ideal measure of stress. During a stress response they are released prior to cortisol and represent a more immediate response. However, this very attribute (represented by a rapid and transient rise) makes it difficult to accurately measure catecholamine levels and capture the stress response (Hofer and East, 1998). Although there are also considerations when measuring glucocorticoid levels, they are certainly one of the most frequently employed indicators of stress (for reviews see Whitten *et al.,* 1998a; Möstl and Palme, 2002; Millspaugh and Washburn, 2004; Strier and Ziegler, 2005; Ziegler and Wittwer, 2005; Honess and Marin, 2006; Keay *et al.*, 2006). Long-term measures of glucocorticoids such as the one employed in this study can identify patterns of stress sensitivity in response to reproductive and seasonal changes, which can ultimately identify selection pressures that have shaped species, and that may in turn affect their future fitness.

Glucocorticoids may fluctuate both seasonally and daily (*black bears*: von der Ohe *et al.*, 2004; *hedgehogs*: Saboureau *et al.,* 1979; *humans*: Wehr 1998; *primates*: Rose *et al.*, 1978, Wilson *et al.*, 1978, Coe and Levine 1995, Sousa and Ziegler, 1998, Stavisky *et al.*, 2001a; *sand rats*: Amirat *et al.*, 1980; *fish*: Fivizzani *et al.*, 1984; de Pedro *et al.*, 1998, for review see Lane, 2006). Seasonal fluctuations may be associated with transitory factors such as reproductive cycle and weight (Schiml *et al.*, 1996; French *et al.*, 2004; Bales, 2005; for review see Reeder and Kramer, 2005 and Keay *et al.*, 2006) or level of mate competition (Perret and Predine, 1984; Bercovitch, 1992; Strier *et al.,* 1999; Lynch *et al.,* 2002). For instance, in species where male competition for females is high, a pre-breeding increase in male body weight, which confers reproductive advantages over other males, is accompanied by cortisol level elevations (Perret and Predine, 1984; Wiebe *et al.,* 1988). Even in species where male competition is low, pre-breeding increases in cortisol may be absent, but breeding season increases still occur (Strier *et al.* 1999; Lynch *et al.* 2002; Tecot, in preparation). In cooperatively breeding New World monkeys (Ziegler *et al.*, 1996, 2004; da Silva Mota *et al.*, 2006) and lemurs (Tecot, 2007a), females' basal cortisol levels increase mid-gestation, and are followed by male elevations which may be associated with infant bonding (Storey *et al.*, 2000; Nunes *et al.*, 2001; Ziegler *et al.*, 2004), stimulating the release of other important parenting hormones necessary for infant care-giving behaviors (Ziegler, 2000; Fleming *et al.*, 2002).

Investigations into the ecological correlates of cortisol secretion are less common than studies of social influences. However, annual changes in cortisol levels have been associated with seasonal changes in weather, resource distribution and availability, and habitat quality (Astheimer *et al.* 1995; Strier *et al.* 1999; Foley *et al.*, 2001; Huber *et al.*, 2003; Pride, 2005; Chapman *et al.,* 2006). For instance, cortisol levels increased in

African elephants *(Loxodonta africana)* with declining food, water, and body condition (Foley *et al.,* 2001), and in red deer *(Cervus elaphus)* with snow and declining temperatures (Huber *et al.*, 2003).

Daily fluctuations in glucocorticoid production are normal (e.g., Fulkerson and Tang, 1979 [sheep]; Cavigelli *et al.*, 2005 [mice]) and occur under control of the biological clock to help regulate metabolic activity (Dallman, 1993; Dallman *et al.*, 1993) and *maintain* homeostasis. Although age (Gust *et al.*, 2000) and social status (Cross and Rogers, 2004) may have additional effects upon diurnal patterns of cortisol secretion, the typical mammalian pattern of corticoid (corticosterone or cortisol) secretion, also seen in some non-mammalian species (e.g., sparrows: Breuner *et al.*, 1999; Romero and Remage-Healey, 2000), consists of peak corticoid levels at or just prior to first activity (Wilson *et al.*, 1978; Czekala *et al.,* 1984; Rusak, 1989; Coe and Levine, 1995; Sousa and Ziegler, 1998; Stavisky *et al.*, 2001b; but see Fulkerson and Tang, 1979). Corticoid levels are highest in the morning in diurnal species and in the evening in nocturnal species, and peak levels are often coincident with the onset of locomotion. Patterns of cortisol excretion in diel and cathemeral species have not been studied (Tecot, in preparation). Increased levels are not a result of activity, however, as these increases in corticoid levels appear to be cued by circadian clocks in the same way that activity patterns are maintained in species; a corticoid surge enables the mobilization of energy required for the demands of the active period. Subsequently, mammalian basal corticoid levels remain somewhat elevated throughout the day and gradually decline (Coe and Levine, 1995; Whitten *et al.*, 1998a). Daily troughs in corticoid levels typically occur with the onset of inactivity and remain low until the pre-activity elevation.

Primates and Stress

Primates may be particularly susceptible to reduced reproductive success from ecological and social pressures due to the slower life-history patterns characteristic of this order. Primates generally produce relatively few offspring in a lifetime, who mature slowly and are dependent for an extended time (Charnov and Berrigan, 1993). Increased time and energetic requirements for reproduction and the survival of offspring relative to other mammals make this group particularly sensitive to physiological stress (Tilden and Oftedal, 1995). Reproductive strategies are ultimately determined by the ability of an individual to acquire enough food resources for itself and its offspring (see above). As environmental and social stressors can inhibit reproduction (Mendoza and Mason, 1988; Sapolsky, 1992; Abbott *et al.,* 1998, 2003; Wingfield and Sapolsky, 2003), the lifetime reproductive success of primates impacted by these stressors may be reduced more severely than in other, faster reproducing mammals.

Cortisol in Primates

In general, investigations of the primate adrenocortical response have determined that unpredictability elicits cortisol level elevations. Captive female cotton-top tamarins *(Saguinus oedipus)* had higher urinary cortisol levels when moved into novel social environments than when housed in natal groups (Ziegler *et al.,* 1995), suggesting that unpredictable social conditions are stressful. Numerous studies of the hormonal correlates of dominance have met with varied results, where dominant individuals have either higher (Sapolsky, 1991) or lower (Chamove and Bowman, 1978; Sapolsky, 1983; Kaplan, 1986) cortisol levels, or there is no relationship between rank and cortisol at all (Sapolsky, 1983; Gust *et al.*, 1993). The stability of the hierarchy appears to be the best predictor of cortisol (Sapolsky, 1992). For instance, the alpha individual may have high

cortisol levels in an unstable group where the unpredictability of becoming ousted and increased aggression may cause increased stress. The same individual may have low cortisol levels during group stability where aggression is infrequent and access to resources is relatively easy (Sapolsky, 1991).

Social structure can also predict adrenal activation because of this relationship between unpredictability and stress. For example, titi monkeys live in socially monogamous, territorial groups and had greater adrenal sensitivity to environmental novelty, such as changes in sound, smell, or cage, compared with squirrel monkeys which live in multi-male and female groups (Hennessy *et al.,* 1995). In titi monkeys, a slight change in novelty elicited cortisol level elevations and small incremental changes in novelty were reflected in cortisol levels. Conversely, considerable changes in novelty were required for an adrenal response in squirrel monkeys. Hennessy and colleagues (1995) suggest that the difference in adrenal sensitivity between these two species is due to the fact that titi monkeys experience novelty to a lesser degree in their social groups. For instance, while squirrel monkeys venture into new environments or take variable routes to reach resources, titi monkeys tend to remain within their familiar territories and live in groups in which membership is stable. Hence, titi monkeys may not be well adapted to a squirrel monkey lifestyle, but their sensitivity enables them to survive in and protect a known territory.

Environmental unpredictability may have a similar effect. In captive squirrel monkeys, predictable, optional foraging tasks promoted psychological well-being; unpredictable foraging demands were chronic stressors, requiring increased energy expenditure, and resulting in prolonged, increased levels of cortisol (Champoux *et al.,* 1993). Adrenal activation may thus be sustained in seasonal environments where, for

instance, resource availability is unpredictable or scarcity is prolonged. While cortisol levels in one free-ranging *Lemur catta* group did not change seasonally with food availability, those in a drier and less predictable habitat did (Cavigelli, 1999).

Regular seasonal environmental fluctuations may also impact cortisol levels as energy stores are mobilized when energy in the environment becomes less available and/or more energy is needed for activities such as acquiring food or thermoregulation. For instance, high cortisol levels were found during the lean season in baboons (Sapolsky, 1986) and ring-tailed lemurs (Cavigelli, 1999; also suggested in Pride, 2005). Similarly, higher cortisol levels were excreted during the cold season in chacma baboons (Weingrill *et al.,* 2004), and suggest that this response helped this species avoid thermal stress. Yet, it is unknown how primates respond to environmental stochasticity without the influence of socially mediated hormone changes.

Lemur Stress: Models of Lemur Evolution

Analyses of the response to stress can help test evolutionary models that propose ecological stress as an adaptive force causing unique lemur behavior and physiology. It has been hypothesized that Madagascar's environment has strongly influenced lemur evolution (Smith and Ganzhorn, 1996). Lemurs possess many unique traits compared with other primates, such as cathemerality (polyphasic activity pattern throughout a 24-hour cycle; Tattersalll, 1987), synchronized breeding with very short estrus periods and a breeding season ("a discrete period of the year to which all births are confined" Lancaster and Lee, 1965, p. 488), low basal metabolic rate (Kurland and Pearson, 1986; Snodgrass *et al.*, 2007), and monomorphy (Jolly, 1966; Wright, 1999). Historically researchers hypothesized that these traits were the result of reproductive stress (Jolly, 1984; Richard and Nicoll, 1987; Richard and Dewar, 1991). Young *et al.* (1990) postulated that lemur

females undergo high energetic burden during reproduction (gestation and lactation) relative to the available energy in the environment. However, in comparison with other primates, postnatal reproduction in lemurs is not particularly energetically expensive (Kappeler, 1996; but see Godfrey *et al.*, 2004), and more recent studies attribute these traits primarily to environmental or nutritional stress (Tilden and Oftedal, 1995; Kappeler, 1996; Wright, 1999); lemur traits may help lemurs *avoid* reproductive stress (Tilden and Oftedal, 1995; Pereira *et al.,* 1999).

Lemurs can be quite flexible, however, and their behavior is subject to modifying factors. For instance, the unique lemur traits associated with reproduction can vary in response to the environment, and may help alleviate stress. Several researchers have reported wide birth peaks lasting as long as 3 months (*e.g.,* Budnitz and Dainis, 1975; see also Whitten and Brockman, 2001; Tecot and Overdorff, 2005), supra-annual aseasonal breeding where births occur in several different months from year to year (*e.g.,* Mutschler, 1999; Tecot and Overdorff, 2005; for reviews see Whitten and Brockman, 2001 and Brockman and van Schaik, 2005), and births occurring more often than once per year (Tecot and Overdorff, 2005). The source and extent of this flexibility is unknown, and is suggested to be directly related in part to the physical environment (Whitten and Brockman, 2001). Malagasy lemurids and indriids may employ different growth and reproductive strategies based upon their different diets (Godfrey *et al.,* 2004), and the availability of food most likely does have an effect on reproductive behavior. As a group, these species may differ substantially from other primates because of Madagascar's specific environmental stressors (Wright, 1999; Godfrey *et al.,* 2004).

Two environmental factors that make Madagascar distinct from other regions are its climate and habitat fragmentation. Madagascar's climate is historically harsh and

unpredictable, with frequent droughts, cyclones, and frosts (Ganzhorn, 1995a; Sauther, 1998; Ganzhorn *et al.,* 1999a; Wright, 1999). There is seasonal variation in fruiting peaks, long periods of fruit unavailability, low soil fertility, slow tree growth, and small tree crown diameter, particularly in the eastern rainforests (Morland, 1991; Overdorff, 1993a, 1996a; Hemingway, 1995; Overdorff and Strait, 1998; Ganzhorn *et al.,* 1999ab). Additionally, cyclones frequently kill immature trees and inhibit fruiting, further reducing the predictability of resource availability (Hemingway, 1995; Wright, 1995; Sauther, 1998). Wright's (1999) energy frugality hypothesis (EFH) proposes that the harsh, unpredictable environment in which lemurs live contrasts with other primate habitats, and this environment selected for the evolution of unique traits, which conserve energy (Jolly, 1984), and maximize food resources (Table 1.1). For instance, small group sizes may be an energy conservation strategy that allows scarce resources in small tree crowns to last longer (Ganzhorn *et al.,* 1999b) and reduce competition within the group (Wright, 1995; 1999). Cathemerality is a resource maximization strategy that may provide temporal flexibility in foraging, optimizing the exploitation of food resources during times of greatest abundance and quality, and low predation risk (Rasmussen, 1999).

Table 1.1. Proposed energy conservation and scarce resource maximization traits observed in Lemurids. Based upon the Energy Frugality Hypothesis (Wright, 1999).

Energy Conservation	Scarce Resource Maximization
Small Group Sizes	**Cathemerality**
Torpor	**Territoriality**
Sperm Competition	**Female Dominance**
Low Basal Metabolic Rate	**Fibrous Diet**
Seasonal Breeding	**Weaning Synchrony**

Anthropogenic disturbances have also shaped Madagascar's unique environment. Madagascar has some of the richest primate species diversity, but has suffered a 90% loss of habitat mainly due to logging and agricultural clearing over the past 2000 years, since humans arrived on the island (MacPhee and Burney, 1991; Nelson and Horning, 1993; Mittermeier *et al.,* 2006). In conjunction with climatic factors, anthropogenic disturbances yield fragmented forests with intensified periods of scarce and unpredictable resource availability. Habitat loss often translates to a loss of habitat diversity and more specifically fruit diversity, which can further intensify the effect of the lean season (Terborgh, 1986b). Furthermore, the particular forests that lemurs inhabit are among the most threatened forests in the country (Green and Sussman, 1990). Lemurs in heavily disturbed areas are the most vulnerable to climatic disturbances because forest fragmentation prevents them from dispersing to larger forests (Ganzhorn *et al.,* 1996/7, 1997; Wright, 1999) and induces crowding, intensifying the effects of scarce resources.

Habitat alteration affects the density and distribution of many lemur species (Dagosto, 1989; Harcourt and Thornback, 1990; White *et al.,* 1995; Johnson and

Overdorff, 1999; Grassi, 2001; Irwin, 2006), and intraspecific variation in lemur behavior is evident as a result of the differential resource distribution and abundance caused by forest fragmentation (Harcourt and Thornback, 1990; White *et al.,* 1995; Porter, 1998; Grassi, 2001). Several studies of conspecifics in Madagascar have investigated the behavioral and demographic correlates of habitat composition, and found differences in locomotion style, feeding preference, population density, and group size (Dagosto, 1989; White *et al.,* 1995; Balko, 1998; Johnson and Overdorff, 1999; Nash, 1999; Grassi, 2001, personal communication). In lower quality habitats some species exist in larger groups and higher densities, while others decrease in size and density. While these studies demonstrate inter-site diversity and behavioral flexibility, they also indicate that population density and other measures *alone* are not reliable indicators of stress, nor are they sufficient to indicate fitness risk associated with habitat quality (Hofer and East, 1998; Merenlender *et al.,* 1998).

To determine how lemurs respond to ecological stress in rainforest environments, it is critical to investigate the proximate mechanisms mediating these behaviors. Hormonal studies are the next critical step that must be taken in the field of socioecology to identify which external pressures influence lemurids and how these pressures impact lemurid strategies.

Cavigelli (1999) measured fecal cortisol levels in *Lemur catta* in southwest Madagascar's dry forests to determine behavioral correlates to stress, and found that times of greatest feeding effort were accompanied by increased cortisol levels. However, this was not as strong a predictor as dominance rank or reproductive state. In the absence of detailed phenological and time budget data, and longer-term data spanning several food availability seasons, it was unclear what energetic strategies were employed

(Cavigelli, 1999). For instance, during the lean season animals may delay glucocorticoid excretion until conditions become severe, they may excrete glucocorticoids throughout the season in short bursts, or they may increase glucocorticoid levels immediately upon experiencing a food decline (see Cavigelli, 1999). Furthermore, dominance interactions in this species made it unclear what environmental conditions elicited which energetic strategies.

Noninvasive Measures of Cortisol

Interest in the study of stress in wild animals has increased substantially with the refinement and validation of techniques that can be used in the field. While serum cortisol is an excellent measure of stress and some researchers have been able to collect samples successfully in the wild (Sapolsky, 1982, 1993; Cook *et al.*, 2000), this is not always practical in field situations. Stressors in the natural habitat can be investigated using methodological advances in cortisol acquisition, *e.g.* extraction from feces and urine (Risler *et al.,* 1987; Gross, 1991; Miller *et al.,* 1991; Monfort *et al.,* 1997; Whitten, *et al.,* 1998ab; Cavigelli, 1999; Stavisky *et al.*, 2001b). Despite concerns over the difficulty in collecting fecal and urine samples appropriate for analysis (e.g., Sauerwein *et al.*, 2004), and extensive methodological considerations (Möstl and Palme, 2002; Touma and Palme, 2005; Lane, 2006), researchers have been able to reliably collect, extract, and measure cortisol metabolites in feces and urine in a wide variety of species (including, but not limited to: dogs [Monfort *et al.*, 1997], ewes [Lindner, 1972], felids [Carlstead *et al.*, 1992], mice [Touma *et al.*, 2004], owls [Wasser *et al.*, 1997], primates [Risler *et al.*, 1987; Stavisky *et al.*, 1994, 2001a; Whitten *et al.*, 1998b; Cavigelli, 1999; Tecot, 1999, 2001; McCallister *et al.*, 2004; Gould *et al.*, 2005; Peel *et al.*, 2005], rodents [Harper and Austad, 2002; Zav'yalov *et al.*, 2003; Touma *et al.*, 2004; Cavigelli *et al.*,

2005], rhinos [Carlstead and Brown, 2005], ruminants [Miller *et al.*, 1991; Möstl *et al.*, 2002], squirrels [Mateo and Cavigelli, 2005], sea lions [Mashburn and Atkinson, 2004], sows [Hay and Mormede, 1998], and wallabies [McKenzie and Deane, 2005]). Fecal cortisol profiles have been found to parallel serum cortisol profiles, and fecal cortisol reliably measures adrenal axis activity (e.g., Whitten *et al.*, 1998ab; Palme *et al.*, 1999; Terio *et al.*, 1999; Harper and Austad, 2002; Stavisky, unpublished data). Fecal cortisol is advantageous because it allows the investigation of stressors in the natural habitat that may have an evolutionary impact on species, and eliminates the additional stress associated with capture and venipuncture that may confound results (Dettmer *et al.,* 1996; Bronson, 1999). Fecal steroid analysis is also beneficial because it represents the accumulation of adrenal activation throughout one day (Sayre 1996; Stavisky pers. comm.). This quality facilitates a more precise assessment of the impact of long-term processes compared with point sampling (Harper and Austad, 2000), and provides the best opportunity to examine the adrenal activity of species adopting different activity patterns such as cathemerality (day-night active: Tattersalll 1987). Fecal extractions enable long-term sampling which can account for daily fluctuations, highlight prolonged influences upon an animal's physiology, identify patterns of stress sensitivity in response to seasonal changes, and ultimately identify selection pressures which affect the Darwinian fitness of species.

STUDY SPECIES: THE RED-BELLIED LEMUR

To best discern when the environment exerts stress upon lemurid species and determine how lemurs mitigate that stress, this study investigates seasonal cortisol levels in the red-bellied lemur (*Eulemur rubriventer*). Red-bellied lemur characteristics indicate that they are sensitive to environmental change (see below), and they are thus a good

candidate species for viewing hormonal changes. This is the first long-term ecological investigation of the direct effects of seasonal changes and habitat composition on the physiological stress response in a lemur species. This study will determine the extent of physiological intra-specific variation that ecological stress may cause, and more clearly identify ecological stressors imposing past and current selective pressure. Conducting this study in disturbed and undisturbed habitats with variable predictability in food resources will additionally help determine the ecological conditions under which different energetic strategies are employed. Results from this study have implications for models of lemur evolution, as well as the broader question of how the environment functionally exerts selective pressure on primate species.

Red-bellied lemurs are at high risk of extinction and are listed as 'vulnerable' on the IUCN Red List (IUCN, 2006). Their range extends along the band of rain forest that runs along eastern Madagascar (Figure 1.2) (Irwin *et al.*, 2005), and has decreased in size since earlier censuses, conducted as recently as 1996 (Mittermeier *et al.*, 2006). Only 3% of Madagascar's land is protected, though a recent presidential pledge to triple that area was recently made (UNESCO, 2003). With a high rate of deforestation and low level of habitat protection, estimates of range size based upon data from several years prior are probably tenuous. Infant mortality has been estimated to reach as high as 50% (Mittermeier *et al.*, 2006). They live in small, strictly pair-bonded family groups (Merenlender, 1993; Overdorff and Tecot, 2006), and as a result may be more sensitive to environmental stressors compared with other primates with different social structures (Hennessy *et al.*, 1995). Both adult males (Overdorff, 1991) and juveniles (Tecot and Overdorff, 2005) carry infants for up to 100 days after birth (Mittermeier *et al.*, 2006; Tecot, personal observation), sharing in the energetic burden of the infant with the

reproductive female of the group. Although they are reproductively mature at approximately 1.5 – 2 years of age, age at first reproduction is delayed, averaging 5.5 years (Merenlender, 1993). Twinning has also been observed frequently (Tecot and Overdorff, 2005). Although most frugivorous species distinguish themselves from folivorous species by remaining active for the majority of the day, red-bellied lemurs display an odd combination of frugivory and extensive bouts of sleeping throughout the day (Overdorff, 1988; Tecot, personal observation).

This species is ideal for the study of the selective pressures exerted by Madagascar's environment on lemurs for several reasons. First, red-bellied lemurs possess many of the unique prosimian traits proposed to have evolved to maximize resources and/or conserve energy, including small groups, cathemerality, exceptionally strict seasonal breeding with short breeding periods, rapid infant development, low basal metabolic rate, and monomorphy (see above) (Kurland and Pearson, 1986; Overdorff, 1988, 1991, 1996ab, 1998; Overdorff and Rasmussen, 1995; Wright, 1999; Snodgrass *et al.*, 2007). Rapid infant development (Overdorff, 1991; Godfrey *et al.*, 2004) coupled with resting metabolic rates below that predicted by the Kleiber scaling relationship (Snodgrass *et al.,* 2007) may further require high energetic investment pre- and post-natally (Richard and Nicoll, 1987; Pereira *et al.,* 1990; Young *et al.,* 1990; Kappeler, 1996; but see Whitten and Brockman, 2001 for a discussion of other important factors in determining reproductive burden) and intensify the effects of resource scarcity at those times. Monomorphy (Kappeler, 1991), in addition to its proposed benefit in extreme environments, enables comparisons between the sexes while eliminating the introduction of confounding metabolic- or other size-associated factors (Clutton-Brock *et al.*, 1977; Strier, 1987; Vasey, 2005).

Second, an analysis of the effects of resource seasonality is best conducted with a species whose preferred diet is patchy in time and space, and red-bellied lemurs subsist mainly upon fruit (Overdorff, 1993, 1996ab; Tecot, this study). A frugivorous diet is commonly associated with high sensitivity to habitat modification (Johns and Skorupa, 1987; Marsh *et al.* 1987; Richard and Sussman 1987; Struhsaker 1997; Harcourt 1998), so both seasonal and site differences are also best observed in a frugivorous species. In fact, red-bellied lemurs have been found to respond to seasonal environmental changes by adjusting their behaviors, increasing foraging time, leaping more, and walking less during the dry season (Dagosto, 1989; Overdorff, 1996a).

Third, red-bellied lemurs are monogamous and territorial (Overdorff, 1996a; Overdorff and Tecot, 2006) and may be highly sensitive to environmental stressors because of reduced novelty in group membership in this social/mating system (Hennessy *et al.,* 1995), and the need to respond to intruders. Unlike species with more complex social and mating systems, in which members may be better adapted to group change and novelty, monogamous species are likely to respond more strongly to variability and novelty as stressors (see above).

Fourth, red-bellied lemur adults in established pair-bonds do not emigrate, and aggression is rare (Overdorff, 1996b; Overdorff and Tecot, 2006). In fact rates of aggression are extremely low (0.0004/hr, this study; Overdorff and Tecot, 2006) and aggressive encounters most commonly occur in the context of weaning (Overdorff and Tecot, 2006). Therefore, the chances of losing study animals to migration are decreased, group size will be relatively stable with no immigration if pairs remain together, intense male-male competition is not expected, and hormonal measures during the breeding season and otherwise are not likely to be impacted by the stress of aggressive encounters.

Fifth, red-bellied lemurs range in the eastern rain forests of Madagascar in adjacent disturbed and undisturbed forests, and have high site fidelity (Overdorff and Tecot, 2006; Tecot, personal observation). Red-bellied lemurs do not migrate between these sites, enabling comparisons between different sites while holding climate constant (see below). Furthermore, rainfall in the eastern rainforests is not consistently related to food availability (Atsalis, 1999aa; Overdorff and Wright, unpublished manuscript), thus suggesting some unpredictability in the environment while assisting in viewing the individual effects of climate and resource availability on this species.

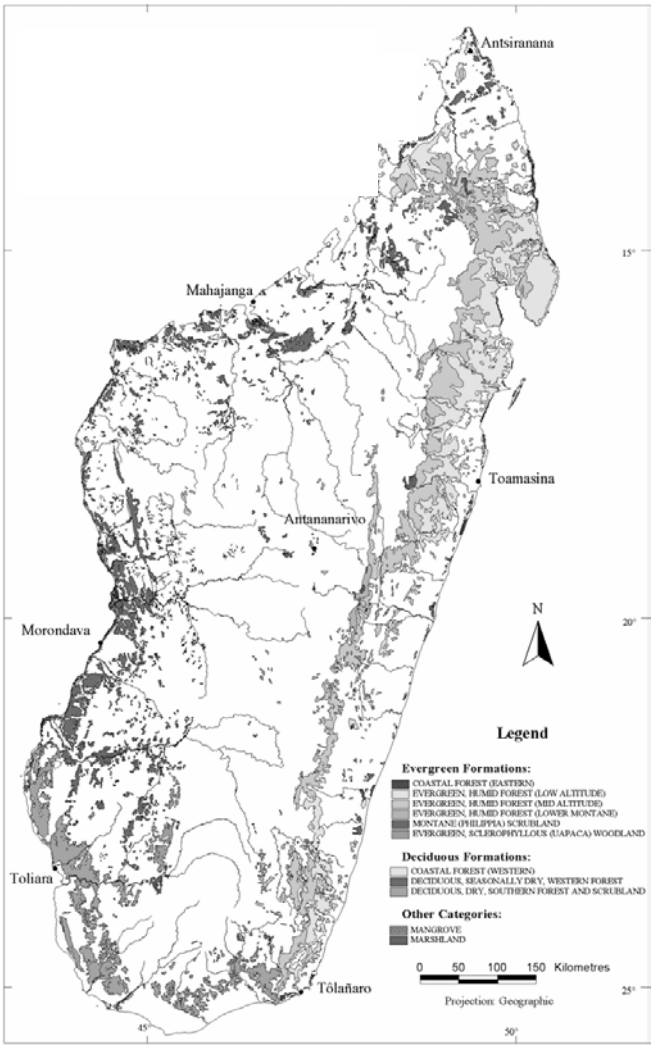


Figure 1.2. Map of Madagascar. Remaining primary vegetation. With the permission of the Trustees of the Royal Botanic Gardens, Kew.

Research Sites

To determine the degree to which habitat has an effect on prosimian fecal cortisol levels across seasons, data were collected for fifteen (behavior) to nineteen (ecology and hormones) months from Talatakely and Vatoharanana, two adjacent sites in Ranomafana National Park (RNP), Madagascar (Figure 1.3). These sites are subject to similar climates but varying levels of habitat alteration. Controlling for climate, the effects of habitat quality can be assessed more readily. As a result of selective logging, the density and abundance of plant species (including those resources preferred by the lemur population) differ significantly between the sites (Turk, 1995; Wright, 1995; Balko, 1998).

RNP consists of approximately 43,500 ha of evergreen rain forest in Fianarantsoa Province, southeast Madagascar (between 21˚02' to 21˚25' S and 47˚18' to 47˚37' E) (Figure 1.3) (DuPuy and Moat, 1995). It is located along the eastern north-south escarpment which causes trade winds to rise and maintains humidity (90%) and moisture (B. Johnson, 2002; DuPuy and Moat, 2003). This park contains the largest known population of red-bellied lemurs (Wright 1992), as well as at least 11 other primate taxa (Wright, 1992). RNP ranges from lowland (500m) to montane rain forest (1500 m), with low soil productivity (B. Johnson, 2002). This area is highly seasonal with distinct wet and cool/dry seasons (Jury, 2003), and large peaks and prolonged troughs in food availability, particularly fruit (Morland, 1991; Overdorff, 1993, 1996a; Hemingway, 1995; Overdorff and Strait, 1998). There is extreme variation in the amount of rainfall (avg. 1500 mm – 4000 mm per year), as well as the lengths of wet and dry seasons, across years (Wright 1992; Overdorff and Wright, unpublished manuscript;). Cyclone

activity typically occurs January through March. Phenological patterns are highly unpredictable from year to year, and the predictability of fruits, flowers, and new leaves can vary dramatically as rainfall is linked with food availability in some years but not consistently (Overdorff and Wright, unpublished manuscript).

Talatakely: At 500m in altitude, this site was heavily logged from 1986 to 1989 when approximately 5,600 ha of timber concessions were granted, and is currently regenerating (Wright, 1992, 1997; Wright and Andriamihaja, 2002). As a result of habitat alteration, this site has been characterized as secondary rain forest with emergent *Eucalyptus* trees (Overdorff, 1988), a discontinuous tree canopy, high tree species diversity and density, and trees small in diameter at breast height (DBH), height, and crown volume compared with those in Vatoharanana (White *et al.*, 1995; Balko, 1998). The understory largely consists of Rubiaceae and Myrsinaceae, bamboo, and epiphytic species (Turk, 1995). Large stands of Chinese guava (*Psidium cattleianum*) have developed since the 1950s and comprise approximately 10% of the 5 km^2 trail system (P. Wright, personal communication). Although this species is competitive and invasive, it has not aggressively spread over the course of the past 20 years (P. Wright, personal communication).

Vatoharanana: This site is located 6 kilometers south of Talatakely, at approximately 1200m in altitude. Although this site was selectively logged and approximately 1,000 trees were removed (Balko, 1998), it has been characterized as continuous primary forest with steep mountain slopes, low tree diversity and density, a continuous canopy, and trees large in dbh, height, and crown volume compared with those in Talatakely (Balko, 1998; Dagosto and Yamashita, 1998; Overdorff, 1988; White *et al.*, 1995; Grassi, 2001). Research at this site was conducted within the 6 km^2 trail

system, as well as an extended trail system constructed during this study and previously by S. Karpanty.

These sites were ideal for this study because they have experienced varying levels of habitat disturbance, yet are subject to similar climates (rainfall and temperature), facilitating inter-site comparisons without the potentially confounding influence of climatic differences.

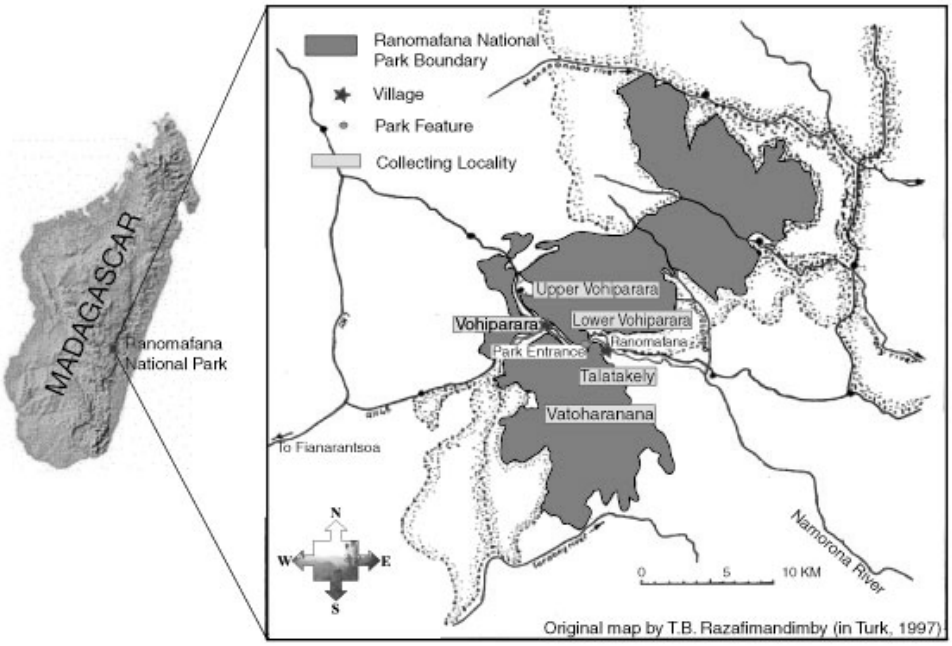


Figure 1.3. Map of Ranomafana National Park, Madagascar. Map from Turk (1997), modified by Elsom (2002). Printed with permission from E. Cunningham (formerly Elsom), CalAcademy.

HYPOTHESES AND PREDICTIONS

This study investigated whether lemurs were ecologically stressed, when they were stressed, and whether they mediated stress by maximizing resources and/or minimizing energy expenditure. Specifically, this study examined how cortisol levels varied with climate, food abundance and habitat quality, and how animals compensated for these changes through dietary and time budget adjustments. Conducting this study in

two sites of variable disturbance helps identify the nature of this species' flexibility and the extent to which flexibility can be maintained without adverse effects. While the following are not mutually exclusive predictions, conducting this study over the course of nineteen months in this unpredictable environment enabled the examination of the individual influences of these seasonal pressures, as well as the interactions among them.

Climate

Climate has implications for both food availability and thermoregulation. I predicted that distinct cool/warm, wet/dry seasons would occur and that seasonal climatic patterns would be reflected in behavior time budgets and cortisol levels such that thermoregulatory adjustments would be made. Since each site was subject to a similar climate, I predicted that seasonal behavioral and hormonal changes would be comparable between sites. Any behavioral and hormonal site differences across climate seasons would indicate the use of different energetic strategies by these populations.

Botany

Previous studies at these sites report differences in habitat structure and species inventory (Balko, 1998), as well as intraspecific variation in lemur behavior (Arrigo-Nelson, 2006). Simultaneous comparisons of these two sites are rare (Balko, 1998), and large-scale assessments of either site are primarily based upon data collected in the late 1980s and 1990s (*e.g.,* Overdorff, 1988, 1991; Balko, 1998), which may not reflect the current state of these sites. I predicted that overall these sites would remain botanically distinct: red-bellied lemur resources would be structurally different, and seasonal plant phenology (food abundance and scarcity seasons) would not be synchronized. Furthermore, I predicted that plant phenology would be less seasonal and more unpredictable from month to month in the disturbed site (Talatakely), with extended

depressions in preferred, high quality foods and high variation in availability from month to month.

Behavior

Flexible foraging strategies may serve as behavioral coping strategies in response to scarce resources and reduce the need for adrenocortical activation (Watson *et al.*, 1999). Food may be maximized and/or energy may be conserved by adjusting the relative time spent feeding, resting, and traveling. Behavioral data were collected to understand how this species mitigates seasonal stress. Seasonal comparisons of time budgets were conducted to elucidate behavioral adjustment strategies employed by this species, and site comparisons were conducted to highlight the flexibility of strategies in response to differential habitat structure. Previous research indicates that this species spends 74-83% of their time resting (Durham, 2003), and they therefore appear to display an energy conservation strategy (minimizing energy expenditure on feeding and traveling). I predicted that this pattern would be more extreme (more resting would occur relative to other behaviors) during cold, wet, and resource-poor seasons. Furthermore, I predicted that these seasonal responses would be similar in each site, yet intensified in the disturbed site (Talatakely).

Hormones

Cortisol levels were analyzed to (1) determine when lemurs increase energy expenditure, and (2) compare fluctuations in cortisol excretion profiles between sites to identify the impact of the habitat. Fecal cortisol levels respond to changes in season as measured by rainfall in muriqui males (Strier *et al.,* 1999), where rainfall is a good predictor of food availability. In SE Madagascar rainfall and food availability are not clearly correlated (Hemingway, 1998), and food availability is expected to be a stronger

influence than rainfall on cortisol levels. However, I predicted that changes in temperature, rainfall, and food availability would be reflected in fecal cortisol levels, and patterns of cortisol excretion throughout the study would be similar in each site insofar as they respond to climate and food. I also predicted that responses to these changes would be more extreme in the disturbed site (Talatakely) such that the magnitude and duration of cortisol elevations would be greater and prolonged compared with the undisturbed site (Vatoharanana).

AIMS OF THE STUDY

This study uses a novel combination of noninvasive measures of stress and traditional ecological and behavioral sampling techniques to yield quantitative measures of environmental impact on lemurs. Little is known about the stress response to food declines and habitat alteration in natural habitats. This study will be one of the first to use these methods to make intra-specific comparisons of stress levels relative to habitat quality; the first in the eastern rainforests of Madagascar. Constructing hormonal profiles throughout different seasons will enhance our understanding of adaptation in primates. Hormonal profiles of Malagasy primates will provide a basis for comparison with primates from other regions not subject to Madagascar's unique environment, and contribute to understanding the relationship between the environment and hormonal profiles. To fully understand lemurs' unique traits, further study of the mechanisms selecting for these traits is essential. By identifying potential fitness risks in the environment, this project will inform on evolutionary models that attribute unique lemur behavior and physiology to ecological stress. The value of this study is further enhanced by its relevance and potential contribution for conservation.

In Chapter 2 (Environmental Seasonality: Seasonal Changes in Plant Phenology and Climate in Two Sites in Ranomafana National Park, Madagascar) I establish seasonal patterns and site differences. I describe the history of the research sites and report results on temperature, rainfall, and phenological assessments as they were measured for the duration of this study. Plant species characteristics and inventories for each site are also reported. The results from this chapter establish operational definitions for climate and food availability seasons and habitat structure differences between sites, which are used throughout the remainder of the dissertation.

In Chapter 3 (*Eulemur rubriventer* Energetics*:* The Influences of Climate, Resources, and Habitat on Time Budgets) I describe how time is allocated among different behaviors overall and monthly to understand how red-bellied lemurs mitigate stress. Behavior time budgets are analyzed for seasonal effects (in relation to temperature, rainfall, and phenology), and in reference to energy maximization and conservation strategies. Time budgets are also compared among sites to help interpret site differences observed in fecal cortisol levels and determine the behavioral flexibility of this species.

In Chapter 4 (Fecal Cortisol Levels in *Eulemur rubriventer*: Physiologically Coping with Environmental Heterogeneity) I report the results of validation tests which determine the ability to measure cortisol in red-bellied lemur fecal extracts. I present results on the influence of temperature, rainfall, and food availability seasons on cortisol levels to determine if red-bellied lemurs undergo periods of stress, and identify when they are stressed. Cortisol profiles and seasonal responses are then compared across sites to enhance interpretations of the effect of the environment on the physiology of this species.

Finally, in Chapter 5 I synthesize all results and discuss the implications of my findings for these populations, and more generally lemurs and other primates. I discuss the significance of these results for the study of environmental selection pressures on primates, and suggest further avenues of research.

References

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Amirat, Z., Khammar, F., Brudieux, R. 1980. Seasonal changes in plasma and adrenal concentrations of cortisol, corticosterone, aldosterone, and electrolytes in the adult male sand rat (*Psammomys obesus*). *General and Comparative Endocrinology*. 40(1):36-43.

Arnold, W. and Dittami, J. 1997. Reproductive suppression in male alpine marmots. *Animal Behaviour*. 53(1):53-66.

Arrigo-Nelson, S.J. 2006. *The Impact of Habitat Disturbance on the Feeding Ecology of the Milne-Edwards' Sifaka* (Propithecus edwardsi) *in Ranomafana National Park* [Doctoral Dissertation]. Stony Brook, NY: Stony Brook University. 181 p.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C. 1995. Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior*. 29:442-457.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Bales, K.L., French, J.A., Hostetler, C.M., Dietz, J.M. 2005. Social and reproductive factors affecting cortisol levels in wild female Golden Lion Tamarins *(Leontopithecus rosalia)*. *American Journal of Primatology*. 67:25–35.

Balko, E.A. 1998. *A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by* Varecia variegata variegata *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Syracuse, NY: SUNY-CESF. 245 p.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W., Simpson, A.J. 1992. Habitat use and resource availability in baboons. *Animal Behaviour*. 43:831-844.

Bercovitch, F.B. 1992. Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior*. 26:272-282.

Bercovitch, F.B. and Ziegler, T.E. 2002. Current topics in primate socioendocrinology. *Annual Review in Anthropology*. 31:45-67.

Berger, P.J., Negus, N.C., Sanders, E.H., Gardner, P.D. 1981. Chemical triggering of reproduction in *Microtus montanus*. *Science*. 214(4516):69-70.

Berry, R.J. and Bronson, F.H. 1992. Life-history and bioeconomy of the house mouse. *Biological Reviews of the Cambridge Philosophical Society*. 67(4):519-550.

Boinski, S., Ehmke, E., Kauffman, L., Schet, S., Vreedzaam, A. 2005. Dispersal patterns among three species of squirrel monkeys *(Saimiri oerstedii, S. boliviensis* and *S. sciureus)*: II. Within-species and local variation. *Behaviour*. 142:633-677.

Breuner, C.W., Wingfield, J.C., Romero, L.M. 1999. Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *Journal of Experimental Zoology*. 284(3):334-342.

Bribiescas, R.G. 2001. Reproductive ecology and life history of the human male. *Yearbook of Physical Anthropology*. 44:148-176.

Brockman, D.K. and van Schaik, C.P. 2005. Seasonality and reproductive function. In: D.K. Brockman, C.P. van Schaik and M.A. van Noordwijk, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 269-305.

Bronson, F.H. 1989. *Mammalian Reproductive Biology.* Chicago: University of Chicago Press.

Bronson, F.H. 1995. Seasonal variation in human reproduction: Environmental factors. *The Quarterly Review of Biology*. 70(2):141-164.

Bronson, F.H. 1999. Puberty and energy reserves: a walk on the wild side. In: K. Wallen and J. E. Schneider, editors. *Reproduction in Context*. Cambridge: MIT Press. Pp. 15-34.

Bronson, F.H. and Heideman, P.D. 1994. Seasonal regulation of reproduction in mammals. In: E. Knobil and J. D. Neil, editors. *The Physiology of Reproduction, 2nd ed*. New York: Raven Press.

Budnitz, N. and Dainis, K. 1975. *Lemur catta*: Ecology and Behavior. In: I. Tattersalll and R. W. Sussman, editors. *Lemur biology*. New York: Plenum. Pp. 219–236.

Burrows, R., Hofer, H., East, M.L. 1994. Demography, extinction and intervention in a small population: The case of the Serengeti wild dogs. *Proceedings of the Royal Society of London Series B*. 256:281-292.

Cameron, J.L. 1997. Stress and behaviorally induced reproductive dysfunction in primates. *Seminars in Reproductive Endocrinology*. 15(1):37-45.

Carlstead, K., Brown, J.L., Monfort, S.L., Killens, R., Wildt, D.E. 1992. Urinary monitoring of adrenal responses to psychological stressors in domestic and nondomestic felids. *Zoo Biology*. 11(3):165-176.

Carlstead, K. and Brown, J.L. 2005. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black *(Diceros bicornis)* and white *(Ceratotherium simum)* rhinoceros. *Zoo Biology*. 24(3):215-232.

Carrillo, E., Saenz, J.C., Fuller, T.K. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. *Biological Conservation*. 108(3):317-324.

Cavigelli, S.A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*. 57(4):935-944.

Cavigelli, S.A., Monfort, S.L., Whitney, T.K., Mechref, Y.S., Novotny, M., McClintock, M.K. 2005. Frequent serial fecal corticoid measures from rats reflect circadian and ovarian corticosterone rhythms. *Journal of Endocrinology*. 184(1):153-163.

Chamove, A.S. and Bowman, R.E. 1978. Rhesus plasma cortisol response at four dominance positions. *Aggressive Behavior*. 4:43-55.

Champoux, M., Zanker, D., Levine, S. 1993. Food search demand effort effects on behavior and cortisol in adult female squirrel monkeys. *Physiology and Behavior*. 54:1091-1097.

Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.L., Saj, T.L., Ziegler, T.E. 2006. Do food availability, parasitism, and stress have synergistic effects on Red Colobus populations living in forest fragments? *American Journal of Physical Anthropology*. 131:525-534.

Charnov, E. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.

Charnov, E.L. and Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evolutionary Anthropology*. 1(6):191-194.

Chatterton, R.T., Kazer, R.R., Rebar, R.W. 1991. Depletion of luteal phase serum progesterone during constant infusion of cortisol phosphate in the cynomolgus monkey. *Fertility and Sterility*. 56:547-554.

Chrousos, G.P. 1998. Stressors, stress, and neuroendocrine integration of the adaptive response: The 1997 Hans Selye Memorial Lecture. *Annals of the New York Academy of Sciences*. 851(1):311-335.

Chrousos, G.P., Torpy, D.J., Gold, P.W. 1998. Interactions between the hypothalamic-pituitary-adrenal axis and the female reproductive system: Clinical implications. *Annals of Internal Medicine*. 129:229-240.

Clarke, M.R., Harrison, R.M., Didier, E.S. 1996. Behavioral, immunological, and hormonal responses associated with social change in rhesus monkeys *(Macaca mulatta)*. *American Journal of Primatology*. 39:223-233.

Clutton-Brock, T.H., Harvey, P.H. 1977. *Primate Ecology*. T.H. Clutton-Brock, editor. London: Academic Press.

Clutton-Brock, T.H., Harvey, P.H., Rudder, B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*. 269:797-800.

Coe, C.L., Franklin, D., Smit, E.R., Levine, S. 1982. Hormonal responses accompanying fear and agitation in the squirrel monkey. *Physiology and Behavior*. 29:1051-1057.

Coe, C.L. and Levine, S. 1995. Diurnal and annual variation of adrenocortical activity in the squirrel monkey. *American Journal of Primatology*. 35:283-292.

Coe, C.L. and Scheffler, J. 1989. Utility of immune measures for evaluating psychological well-being in nonhuman primates. *Zoo Biology*. 1:89-99.

Coelho, A.M. 1986. Time and energy budgets. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology*. New York: Alan R. Liss. Pp. 141–166.

Cohen, S. 1988. Psychosocial models of the role of social support in the etiology of physical disease. *Health Psychology*. 7:269-297.

Colwell, M.A., Gratto, C.L., Oring, L.W., Fivizzani, A.J. 1988. Effects of blood sampling on shorebirds: Injuries, return rates and clutch desertions. *Condor*. 90:942-945.

Cook, C.J., Mellor, D.J., Harris, P.J., Ingram, J.R., Matthews, L.R. 2000. Hands-on and hands-off measurement of stress. In: G.P. Moberg and J.A. Mench, editors. *The Biology of Animal Stress*. New York: CABI Publishing. Pp. 123–146.

Coop, R.L. and Holmes, P.H. 1996. Nutrition and parasite interaction. *International Journal of Parasitology*. 26:951-962.

Cotter, R.C. and Gratto, C.J. 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. *Journal of Wildlife Management*. 59:93-98.

Cross, N. and Rogers, L.J. 2004. Diurnal cycle in salivary cortisol levels in common marmosets. *Developmental Psychobiology*. 45(3):134-139.

Cuthill, I.C. and Houston, A.I. 1997. Managing time and energy. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach*. Massachusetts: Blackwell Science. Pp. 97-120.

Czekala, N.M., Lance, V.A., Sutherland-Smith, M. 1984. Diurnal urinary corticoid excretion in the human and gorilla. *American Journal of Primatology*. 34:29-34.

da Silva Mota, M.T., Franci, C.R., de Sousa, M.B.C. 2006. Hormonal changes related to paternal and alloparental care in common marmosets *(Callithrix jacchus)*. *Hormones and Behavior*. 49:293-302.

Daan, S. and Tinbergen, J.M. 1997. Adaptation to Life Histories. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach, Fourth Edition*. Oxford: Blackwell Science. Pp. 311-333.

DaGosto, M. 1989. Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 78:209.

Dagosto, M. and Yamashita, N. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. *Primates*. 39:459-472.

Dallman, M. 2003. Stress by any other name…? *Hormones and Behavior*. 43(1):18-20.

Dallman, M.F. 1993. Stress update: Adaptation of the hypothalamic-pituitary-adrenal axis to chronic stress. *Trends in Endocrinology and Metabolism*. 4(2):62-69.

Dallman, M.F., Strack, A.M., Akana, S.F., Bradbury, M.J., Hanson, E.S., Scribner, K.A., Smith, M. 1993. Feast and famine: Critical role of glucocorticoids with insulin in daily energy-flow. *Frontiers in Neuroendocrinology*. 14(4):303-347.

de Pedro, N., Delgado, M.J., Pinillos, M.L., Alonso-Gomez, A.L., Alonso-Bedate, M. 1998. Daily rhythms in NAT activity, cortisol, glucose, glycogen and catecholamines in tench (*Tinca tinca*). *Polskie Archiwum Hydrobiologii.* 45(3):321-329.

Dettmer, E.L., Phillips, K.A., Rager, D.R., Bernstein, I.S., Fragaszy, D.M. 1996. Behavioral and cortisol responses to repeated capture and venipuncture in *Cebus apella*. *American Journal of Primatology*. 38(4):357-362.

Di Bitetti, M.S. and Janson, C.H. 2000. When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*. 50:109-130.

Dobbin, J.P., Marth, M., McCain, G.A., Martin, R.A., Cousin, K. 1991. Cytokine production and lymphocyte transformation during stress. *Brain Behavior and Immunity*. 5:339-348.

Drent, R.H. and Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea*. 68(1-4):225-252.

Dunbar, R.I.M. 1988. *Primate Social Systems*. Ithaca, New York: Cornell University Press.

DuPuy, D.J., Moat, J. 1995. A refined classification of the primary vegetation based on the underlying geology: Using GIS to map its distribution and to assess its conservation status. In: W.R. Laurenco, editor. *Biogeography of Madagascar*. Paris: Unesco. Pp. 205-218.

DuPuy, D.J. and Moat, J. 2003. Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 51-74.

Durham, D.L. 2003. *Variation in responses to forest disturbance and the risk of local extinction: A comparative study of wild* Eulemurs *at Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Davis: University of California, Davis. 170 p.

Ellison, P.T., Valeggia, C.R., Sherry, D.S. 2005. Human birth seasonality. In: D. K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 379-399.

Elsom, E. 2002. *A Preliminary Inventory of the* Platynini *(Coleoptera: Carabidae) of Ranomafana National Park* [Master's Thesis]. San Francisco: San Francisco State University.

Esch, G.W., Gibbons, J.W., Bourque, J.E. 1975. An analysis of the relationship between stress and parasitism. *American Midland Naturalist*. 93(2):339-353.

Fivizzani, A.J., Spieler, R.E., Noeske, T.A. 1984. The influence of ambient temperature on the daily variation of serum cortisol in the Banded Killifish, *Fundulus diaphanus*. *Journal of Interdisciplinary Cycle Research*. 15(1):3-8.

Fleming, A.S., Corter, C., Stallings, J., Steiner, M. 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*. 42:399-413.

Foley, C.A.H., Papageorge, S., Wasser, S.K. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*. 15(4):1134-1142.

French, J.A., Koban, T., Rukstalis, M., Ramirez, S.M., Bardi, M., Brent, L. 2004. Excretion of urinary steroids in pre- and postpartum female baboons. *General and Comparative Endocrinology*. 137(1):69-77.

Fulkerson, W.J. and Tang, B.Y. 1979. Ultradian and circadian rhythms in the plasma concentration of cortisol in sheep. *Journal of Endocrinology*. 81(1):135-141.

Ganzhorn, J., Wright, P., Ratsimbazafy, H. 1999b. Primate communities: Madagascar. In: J.G. Fleagle, C.H. Janson and K. Reed, editors. *Primate Communities*. Cambridge: Cambridge University Press. Pp. 75-89.

Ganzhorn, J.U. 1995a. Cyclones over Madagascar: Fate or fortune? *Ambio*. 24:124-125.

Ganzhorn, J.U., Malcomber, S., Andrianantoanina, O., Goodman, S.M. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica*. 29(3):331-343.

Ganzhorn, J.U., Fietz, J., Rakotovao, E., Schwab, D., Zinner, D. 1999a. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*. 13:794-804.

Ganzhorn, J.U., Langrand, O., Wright, P.C., O'Connor, S., Rakotosamimanana, B., Feistner, A.T.C., Rumpler, Y. 1996/7. The state of lemur conservation in Madagascar. *Primate Conservation*. 17:70-86.

Glessner, K.D.G. and Britt, A. 2005. Population density and home range size of *Indri indri* in a protected low altitude rain forest. *International Journal of Primatology*. 26(4):855-872.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*. 123:250-276.

Gould, L., Ziegler, T.E., Wittwer, D.J. 2005. Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs *(Lemur catta)* at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*. 67(1):5-23.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Green, G.M. and Sussman, R.W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*. 248:212-215.

Gross, T. 1991. Development and use of fecal steroid analyses in captive exotic mammals and birds. *Society for Theriogenology, Proceedings of Annual Meeting*: Pp. 66-74.

Gust, D.A., Gordon, T.P., Hambright, M.K. 1993. Response to removal from and return to a social group in adult male rhesus monkeys. *Physiology & Behavior*. 53(3):599-602.

Gust, D.A., Gordon, T.P., Wilson, M.E., Brodie, A.R., Ahmed-Ansari, A., McClure, H.M. 1996. Group formation of female pigtail macaques *(Macaca nemestrina)*. *American Journal of Primatology*. 39:263-273.

Gust, D.A., Wilson, M.E., Stocker, T., Conrad, S., Plotsky, P.M., Gordon, T.P. 2000. Activity of the hypothalamic-pituitary-adrenal axis is altered by aging and exposure to social stress in female rhesus monkeys. *Journal of Clinical Endocrinology and Metabolism*. 85(7):2556-2563.

Halle, S. and Stenseth, N.C. 2000. *Activity Patterns of Small Mammals: An Ecological Approach*. Berlin: Springer.

Harcourt, A. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: T Caro, editor. *Behavioral Ecology and Conservation Biology*. New York: Oxford University Press. Pp. 56-79.

Harcourt, C. and Thornback, J. 1990. *Lemurs of Madagascar and the Comoros. The IUCN Red Data Book*. Gland, Switzerland: IUCN.

Harlow, H.J., Thorne, E.T., Williams, E.S., Belden, E.L., Gern, W.A. 1987. Cardiac frequency: A potential predictor of blood cortisol levels during acute and chronic stress exposure in Rocky Mountain bighorn sheep *(Ovis canadensis)*. *Canadian Journal of Zoology*. 65:2028-2034.

Harper, J.N. and Austad, S.M. 2002. Fecal glucocorticoids: a noninvasive method of measuring adrenal activity in wild and captive rodents. *Physiological and Biochemical Zoology*. 73:12-22.

Hay, M. and Mormede, P. 1998. Urinary excretion of catecholamines, cortisol and their metabolites in Meishan and Large White sows: validation as a non-invasive and integrative assessment of adrenocortical and sympathoadrenal axis activity. *Veterinary Research*. 29(2):119-128.

Hemingway, C.A. 1995. *Feeding and Reproductive Strategies of* Propithecus diadema edwardsi [Doctoral Dissertation]. Durham: Duke University.

Hemingway C.A. 1998. Selectivity and variability in the diet of Milne-Edwards' sifakas *(Propithecus diadema edwardsi)*: Implications for folivory and seed-eating. *International Journal of Primatology*. 19*:*355-377.

Hemingway, C.A. and Bynum, N. 2005. The influence of seasonality on primate diet and ranging. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 57-104.

Hennessy, M.B., Mendoza, S.P., Mason, W.A., Moberg, G.P. 1995. Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*. 57(2):331-338.

Hennessy, M.B., Heybach, J.P., Vernikos, J., Levine, S. 1979. Plasma corticosterone concentrations sensitively reflect levels of stimulus intensity in the rat. *Physiology and Behavior*. 22:821-825.

Hofer, H. and East, M.L. 1998. Biological conservation and stress. In: A.P. Møller, M. Milinski and P.J.B. Slate, editors. *Advances in the Study of Behavior, Vol 27*. San Diego: Academic Press. Pp. 405-525.

Honess, P.E. and Marin, C.M. 2006. Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews*. 30(3):390-412.

Huber, S., Palme, R., Arnold, W. 2003. Effects of season, sex, and sample collection on concentrations of fecal cortisol metabolites in red deer *(Cervus elaphus)*. *General and Comparative Endocrinology*. 130(1):48-54.

Irwin, M.T. 2006. *Ecological Impacts of Forest Fragmentation on Diademed Sifakas* (Propithecus diadema) *at Tsinjoarivo, eastern Madagascar: Implications for*

Conservation in Fragmented Landscapes [Doctoral Dissertation]. Stony Brook, New York: Stony Brook University. 410 p.

Irwin, M.T., Johnson, S.E., Wright, P.C. 2005. The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx*. 39(2):204-218.

IUCN. 2006. *2006 IUCN Red List of Threatened Species*.

Janson, C. and Verdolin, J. 2005. Seasonality of primate births in relation to climate. In: D.K. Brockman, C.P. van Schaik and M.A. van Noordwijk, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 307-350.

Johns, A.D. and Skorupa, J.P. 1987. Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*. 8(2):157-191.

Johnson, B.K. 2002. *Soil characterization and reconnaissance survey of the Ranomafana National Park area, southeastern Madagascar* [Doctoral Dissertation]. Raleigh, NC: North Carolina State University.

Johnson, S.E. 2002. *Ecology and Speciation in Brown Lemurs: White-collared Lemurs* (Eulemur albocollaris) *and Hybrids* (Eulemur albocollaris *X* Eulemur fulvus rufus) *in Southeastern Madagascar* [Doctoral Dissertation]. Austin: University of Texas at Austin. 288 p.

Johnson, S.E. and Overdorff, D.J. 1999. Census of brown lemurs (*Eulemur fulvus* spp.) in southeastern Madagascar: Methods-testing and conservation implications. *American Journal of Primatology*. 47(1):51-60.

Jolly, A. 1966. *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.

Jolly, A. 1984. The puzzle of female feeding priority. In: M. Small, editor. *Female Primates: Studies by Women Primatologists*. New York: Alan R. Liss. Pp. 197-215.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*. 78(1):57-66.

Jury, M.R. 2003. The climate of Madagascar. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 75-87.

Kaplan, J.R. 1986. Psychological stress and behavior in nonhuman primates. In: G. Mitchell and J. Erwin, editors. *Comparative Primate Biology*. New York: Alan R. Liss.

Kappeler, P.M. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*. 57(3):132-146.

Kappeler, P.M. 1996. Causes and consequences of life-history variation among strepsirhine primates. *American Naturalist*. 148:868-891.

Keay, J.M., Singh, J., Gaunt, M.C., Kaur, T. 2006. Fecal glucocorticoids and their metabolites as indicators of stress in various mammalian species: A literature review. *Journal of Zoo and Wildlife Medicine*. 37(3):234-244.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, D., Dale, B.W., Stephenson, T.R. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management*. 64:450-462.

Keller, S.E., Weiss, J.M., Schleifer, S.L., Miller, N.E., Stern, M. 1983. Stress-induced suppression of immunity in adrenalectomized rats. *Science*. 221:1301-1304.

Keuroghlian, A. 2003. *The Response of Peccaries to Seasonal Fluctuations in an Isolated Patch of Tropical Forest* [Doctoral Dissertation]. Reno, Nevada: University of Nevada, 158 p.

Khansari, D.N., Murgo, A.J., Faith, R.E. 1990. Effects of stress on the immune system. *Immunology Today*. 11:170-175.

Knott, C.D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*. 19:1061-1079.

Krebs, J.R. and Davies, N.B. 1997. *Behavioural Ecology: An Evolutionary Approach*. Massachusetts: Blackwell Science.

Kurland J.A., and Pearson J.D. 1986. Ecological significance of hypometabolism in nonhuman primates: Allometry, adaptation, and deviant diets. *American Journal of Physical Anthropology*. 71:445–457.

Lack, D. 1950. The breeding seasons of European birds. *Ibis*. 92:288-316.

Lancaster, J.B. and Lee, R.B. 1965. The annual reproductive cycle in monkeys and apes. In: I. DeVore, editor. *Primate Behavior: Field Studies of Monkeys and Apes*. New York: Holt, Rinehart and Winston.

Lane, J. 2006. Can non-invasive glucocorticoid measures be used as reliable indicators of stress in animals? *Animal Welfare*. 15(4):331-342.

Laudenslager, M.L., Ryan, S.M., Drugan, R.C., Hyson, R.L., Maier, S.F. 1983. Coping and immunosuppression: Inescapable but not escapable shock suppresses lymphocyte proliferation. *Science*. 221:568-570.

Lee, A.K. and Cockburn, A. 1985. *Evolutionary Ecology of Marsupials*. Cambridge: Cambridge University Press.

Lewis, R.J. and Kappeler, P.M. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*. 67(3):347-364.

Lindburg, D.G. 1987. Seasonality of reproduction in primates. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology Vol. 2B Behavior, cognition and motivation*. New York: Alan R. Liss. Pp. 167–218.

Lindner, H.R. 1972. Enterohepatic circulation and patterns of urinary excretion of cortisol metabolites in the ewe. *Journal of Endocrinology*. 52:19-20.

Lynch, J.W., Ziegler, T.E., Strier, K.B. 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male Tufted Capuchin monkeys, *Cebus apella nigritus*. *Hormones and Behavior*. 41:275-287.

MacArthur, R.H. and Pianka, E.R. 1966. On the optimal use of a patchy environment. *American Naturalist*. 100(916):603-609.

MacPhee, R.D.E. and Burney, D.A. 1991. Dating of modified femora of extinct dwarf hippopotamus from southern Madagascar: Implications for constraining human colonialism and vertebrate extinction events. *Journal of Archaeological Science*. 18:695-706.

Marsh, C.W., Johns, A.D., Ayres, J.M. 1987. Effects of habitat disturbance on rain forest primates. In: C.W. Marsh and R.A. Mittermeier, editors. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 83-107.

Mashburn, K.L. and Atkinson, S. 2004. Evaluation of adrenal function in serum and feces of Steller sea lions *(Eumetopias jubatus)*: influences of molt, gender, sample storage, and age on glucocorticoid metabolism. *General and Comparative Endocrinology*. 136(3):371-381.

Mateo, J.M. and Cavigelli, S.A. 2005. A validation of extraction methods for noninvasive sampling of glucocorticoids in free-living ground squirrels. *Physiological and Biochemical Zoology*. 78(6):1069-1084.

May, R.M. and Rubenstein, D.I. 1985. Reproductive strategies. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals: Reproductive Fitness, Book 4*. New York: Cambridge University Press. Pp. 1-23.

McCallister, J.M., Smith, T.E., Elwood, R.W. 2004. Validation of urinary cortisol as an indicator of hypothalamic-pituitary-adrenal function in the bearded emperor tamarin (*Saguinus imperator subgrisescens*). *American Journal of Primatology*. 63(1):17-23.

McEwen, B.S. and Wingfield, J.C. 2003a. The concept of allostasis in biology and biomedicine. *Hormones and Behavior*. 43(1):2-15.

McEwen, B.S. and Wingfield, J.C. 2003b. Response to commentaries on the concept of allostasis. *Hormones and Behavior*. 43(1):28-30.

McKenzie, S. and Deane, E.M. 2005. Faecal corticosteroid levels as an indicator of well-being in the tammar wallaby, *Macropus eugenii*. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology*. 140(1):81-87.

McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist*. 116:106-124.

Mendoza, S.P. and Mason, W.A. 1988. Behavioral and endocrine consequences of heterosexual pair formation in squirrel monkeys. *Physiology and Behavior*. 46:597-603.

Merenlender, A., Kremen, C., Rakotondratsima, M., Weiss, A. 1998. Monitoring impacts of natural resource extraction on lemurs of the Masoala Peninsula, Madagascar. *Conservation Ecology* 2(2):5-29.

Merenlender, A.M. 1993. *The Effects of Sociality on the Demography and Genetic Structure of* Lemur fulvus rufus *(Polygamous) and* Lemur rubriventer *(Monogamous) and the Conservation Implications* [Doctoral Dissertation]. Rochester, New York: University of Rochester.

Miller, M.W., Hobbs, N.T., Sousa, M.C. 1991. Detecting stress responses in Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*): Reliability of cortisol concentrations in urine and feces. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 69(1):15-24.

Millspaugh, J.J. and Washburn, B.E. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *General and Comparative Endocrinology*. 138(3):189-199.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersalll, I., Meyers, D.M. 2006. *Lemurs of Madagascar. 2nd Edition*. Washington, DC: Conservation International.

Monfort, S.L., Wasser, S.K., Mashburn, K.L., Burke, M., Brewer, B.A., Creel, S.R. 1997. Steroid metabolism and validation of noninvasive endocrine monitoring in the African wild dog *(Lycaon pictus)*. *Zoo Biology*. 16(6):533-548.

Morland, H.S. 1991. Preliminary report on the social organization of ruffed lemurs *(Varecia variegata variegata)* in a northeast Madagascar rainforest. *Folia Primatologica*. 56:157-161.

Morton, E.S. 1977. Intratropical migration in the Yellow-green Vireo and Piratic Flycatcher. *The Auk*. 94:97-106.

Möstl, E., Maggs, J.L., Schrotter, G., Besenfelder, U., Palme, R. 2002. Measurement of cortisol metabolites in faeces of ruminants. *Veterinary Research Communications*. 26(2):127-139.

Möstl, E. and Palme, R. 2002. Hormones as indicators of stress. *Domestic Animal Endocrinology*. 23(1-2):67-74.

Muehlenbein, M.P. 2006. Intestinal parasite infections and fecal steroid levels in wild chimpanzees. *American Journal of Physical Anthropology*. 130:546-550.

Mutschler, T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur *(Hapalemur griseus alaotrensis)*. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Press. Pp. 221–239.

Nash, L.T. 1998. Vertical clingers and sleepers 1 : Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*. 69(S1):204-217.

Nash, L.T. 1999. Factors influencing census results on *Lepilemur* and *Microcebus* in southwestern Madagascar. *American Journal of Physical Anthropology*. S28:209.

Negus, N.C. and Berger, P.J. 1972. Environmental factors and reproductive processes in mammalian populations. In: J.T. Velardo and B.A. Kasprow, editors. *Biology of Reproduction: Basic and Clinical Studies*. *Third Pan American Congress on Anatomy*, New Orleans. Pan American Association of Anatomy. Pp. 89-98.

Negus, N.C. and Berger, P.J. 1987. Mammalian reproductive physiology: Adaptive responses to changing environments. *Current Mammalogy, Volume 1*. New York: Plenum Press. Pp. 149-173.

Nelson, R. and Horning, N. 1993. AVHRR-LAC estimates of forest area in Madagascar, 1990. *International Journal of Remote Sensing*. 14:1463-1475.

Nelson, R.J., Demas, G.E., Klein, S.L., Kriegsfeld, L.J. 2002. *Seasonal Patterns of Stress, Immune Function, and Disease*. Cambridge University Press.

Nelson, R.J. and Klein, S.L. 1999. Environmental and social influences on seasonal breeding and immune function. In: K. Wallen and J.E. Schneider, editors. *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior*. Cambridge: MIT Press Pp. 219-256.

Nunes, S., Fite, J.E., Patera, K.J., French, J.A. 2001. Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets *(Callithrix kuhli)*. *Hormones and Behavior*. 39:70-82.

Overdorff, D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D., Merenlender, AM, Talata, P, Telo, A, Forward, AZ. 1999. Life history of *Eulemur fulvus rufus* from 1988-1997: Implications for ecological stress in southeastern Madagascar. *American Journal of Physical Anthropology* 108:295-310.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40(4):327-342.

Overdorff, D.J. 1996b. Ecological correlates to social structure in two Lemur species in Madagascar. *American Journal of Physical Anthropology*. 100(4):487-506.

Overdorff, D.J. 1991. *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral dissertation]. Durham: Duke University. 313 p. Durham: Duke University. 313 p.

Overdorff, D.J. 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. *International Journal of Primatology*. 14(5):721-753.

Overdorff, D.J., Tecot, S. R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 235-245.

Overdorff, D.J. and Rasmussen, M.A. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 61-74.

Overdorff, D.J. and Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Palme, R., Robia, C., Messmann, S., Hofer, J., Möstl, E. 1999. Measurement of faecal cortisol metabolites in ruminants: a non-invasive parameter of adrenocortical function. *Wiener Tierarztliche Monatsschrift*. 86(7):237-241.

Passamini, M. 1998. Activity budget of Geoffroy's Marmoset *(Callithrix geoffroyi)* in an Atlantic forest in Southeastern Brazil. *American Journal of Primatology*. 46:333-340.

Paterson, A.M. and Pearce, G.P. 1992. Growth response to humans and corticosteroids in male pigs housed individually and subjected to pleasant, unpleasant or minimal handling during rearing. *Applied Animal Behavior Science*. 34:315-328.

Peel, A.J., Vogelnest, L., Finnigan, M., Grossfeldt, L., O'Brien, J.K. 2005. Non-invasive fecal hormone analysis and behavioral observations for monitoring stress responses in captive western lowland gorillas *(Gorilla gorilla gorilla)*. *Zoo Biology*. 24(5):431-445.

Pereira, M.E., Kaufman, R., Kappeler, P.M., Overdorff, D.J. 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatologica*. 55:96-103.

Pereira, M.E. 1993. Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 205-221.

Pereira, M.E., Russ, A.S., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Publishers.

Perret, M. and Predine, J. 1984. Effects of long-term grouping on serum cortisol levels in *Microcebus murinus* Prosimii. *Hormones and Behavior*. 18(3):346-358.

Pochron, S.T., Tucker, W.T., Wright, P.C. 2004. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 125:61-72.

Porter, L.M. 1998. Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. *Folia Primatologica*. 69(3):172-176.

Post, E. 2003. Timing of reproduction in large mammals. In: M. D. Schwartz, editor. *Phenology: An Integrative Environmental Science*. Dordecht: Kluwer Academic. Pp. 437-449.

Pride, E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs *(Lemur catta)*. *Behavioral Ecology*. 16(3):550-560.

Rasmussen, D. 1985. A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs *(Lemur* and *Varecia)*. *International Journal of Primatology*. 6(5):501-517.

Rasmussen, M.A. 1999. *Ecological Influences on Activity Cycle in Two Cathemeral Primates,* Eulemur mongoz *(Mongoose Lemur) and* Eulemur fulvus fulvus *(Common Brown Lemur)* [Doctoral Dissertation]. Durham, N.C.: Duke University.

Reeder, D.M. and Kramer, K.M. 2005. Stress in free-ranging mammals: Integrating physiology, ecology, and natural history. *Journal of Mammalogy*. 86(2):225-235.

Richard, A.F. and Dewar, R.E. 1991. Lemur Ecology. *Annual Review of Ecological Systems*. 22:145-175.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild Propithecus verreauxi. *Journal of Human Evolution*. 39(4):381-391.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Richard, A.F. and Nicoll, M.E. 1987. Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology*. 12:309-314.

Richard, A.F. and Sussman, R.W. 1987. Framework for primate conservation in Madagascar. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 329-341.

Richter, H.V. and Cumming, G.S. 2006. Food availability and annual migration of the straw-colored fruit bat *(Eidolon helvum)*. *Journal of Zoology*. 268(1):35-44.

Risler, L., Wasser, S.K., Sackett, G.P. 1987. Measurement of excreted steroids in *Macaca nemestrina*. *American Journal of Primatology*. 12(1):91-100.

Rodway, M.S., Montevecchi, W.A., Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic puffins *(Fratercula arctica)*. *Biological Conservation*. 76:311-319.

Romero, L.M. and Remage-Healey, L. 2000. Daily and seasonal variation in response to stress in captive starlings *(Sturnus vulgaris)*: Corticosterone. *General and Comparative Endocrinology*. 119(1):52-59.

Rose, R.M., Gordon, T., Bernstein, I.S. 1978. Diurnal variation in plasma testosterone and cortisol in rhesus monkeys living in social groups. *Journal of Endocrinology*. 76:67-74.

Rusak, B. 1989. The mammalian circadian system: Models and physiology. *Journal of Biological Rhythms*. 4(2):121-134.

Saboureau, M., Laurent, G., Boissin, J. 1979. Daily and seasonal rhythms of locomotor activity and adrenal function in male hedgehogs *(Erinaceus europaeus)*. *Journal of Interdisciplinary Cycle Research*. 10(4):249-266.

Sadlier, R.M.F.S. 1972. Environmental Effects. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals, Book 4: Reproductive Patterns*. Cambridge: Cambridge University Press. Pp. 69-94.

Saltzman, W., Schultz-Darken, N.J., Scheffler, G., Wegner, F.H., Abbott, D.H. 1994. Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*. 56(4):801-810.

Sapolsky, R.M. 1982. The endocrine stress response and social status in the wild baboon. *Hormones and Behavior*. 16:279–292.

Sapolsky, R.M. 1983. Endocrine aspects of social instability in the olive baboon *(Papio anubis)*. *American Journal of Primatology*. 5:365-379.

Sapolsky, R.M. 1985. Stress-induced suppression of testicular function in the wild baboon: Role of glucocorticoids. *Endocrinology*. 116:2273-2278.

Sapolsky, R.M. 1986. Endocrine and behavioral correlates of drought in the wild baboons. *American Journal of Primatology*. 11:217-226.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons. In: D. Crews, editor. *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*. Englewood Cliffs, New Jersey: Prentice Hall. Pp. 291-322.

Sapolsky, R.M. 1991. Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*. 16(4):281-293.

Sapolsky, R.M. 1992. Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*. 17:701-709.

Sapolsky, R.M. 1992. *Stress, the Aging Brain, and the Mechanisms of Neuron Death*. Cambridge: MIT Press.

Sapolsky, R.M. 1993. Endocrinology alfresco: Psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*. 48:437-468.

Sapolsky, R.M. 1994. *Why Zebras Don't Get Ulcers: A Guide to Stress, Stress-Related Diseases, and Coping*. New York: W.H. Freeman.

Sauerwein, H., Müller, U., Brüssel, H., Lutz, W., Möstl, E. 2004. Establishing baseline values of parameters potentially indicative of chronic stress in red deer *(Cervus elaphus)* from different habitats in western Germany. *European Journal of Wildlife Research*. 50:168–172.

Sauther, M.L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ringtailed lemur conservation. *Folia Primatologica*. 69:309-320.

Sayre, R.W. 1996. *Ecology of bighorn sheep in relation to habitat and oil development in the little Missouri badlands* [Doctoral Dissertation]. Grand Forks, North Dakota: University of North Dakota.

Schapiro, S.J., Bloomsmith, M.A., Kessel, A.L., Shively, C.A. 1993. Effects of enrichment and housing on cortisol response in juvenile rhesus monkeys. *Applied Animal Behaviour Science*. 37(3):251-263.

Schiml, P.A., Mendoza, S.P., Saltzman, W., Lyons, D.M., Mason, W.A. 1996. Seasonality in squirrel monkeys *(Saimiri sciureus)*, social facilitation by females. *Physiology & Behavior*. 60(4):1105-1113.

Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*. 2:369-404.

Schulkin, J. 2003. Allostasis: a neural behavioral perspective. *Hormones and Behavior*. 43(1):21-27.

Selye, H. 1950. *Stress*. Montreal: ACTA, Incorporated.

Selye, H. 1956. *The Stress of Life*. New York: McGraw-Hill.

Selye, H. 1980. *Selye's Guide to Stress Research, Vol.1*. New York: Van Nostrand Reinhold Company.

Smith, A.P. and Ganzhorn, J.U. 1996. Convergence and divergence in community structure and dietary adaptations in Australian possums and gliders and Malagasy lemurs. *Australian Journal of Ecology*. 21:31-46.

Smith, T.E. and French, J.A. 1997. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets *(Callithrix kuhli)*. *American Journal of Primatology*. 42:253-267.

Smits, L.J., Zielhuis, G.A., Jongbloet, P.H., Straatman, H. 1998. Seasonal variation in human fecundability. *Human Reproduction*. 13(12):3520-3524.

Sousa, M.B.C. and Ziegler, T.E. 1998. Diurnal variation on the excretion patterns of fecal steroids in common marmoset *(Callithrix jacchus)* females. *American Journal of Primatology*. 46(2):105-117.

Stavisky, R.C., Brandenberger, D., Hook, M., Russell, E., Kaplan, J., Whitten, P. 2001b. The effect of menstrual cycle phase on cortisol excretion on female cynomolgus monkeys *(Macaca fascicularis)*. *American Journal of Primatology*. 54(S1):39-40.

Stavisky, R.C., Whitten, P.L., Hammett, D.H., Kaplan, J.R. 2001a. Lake pigments facilitate analysis of fecal cortisol and behavior in group-housed macaques. *American Journal of Physical Anthropology*. 116(1):51-58.

Stavisky, R.C., Wilson, M., Russell, E., Whitten, P.L. 1994. Validation of the fecal extraction method: Correlation of serum and fecal endocrine profiles in rhesus macaques, *Macaca mulatta*. *American Journal of Physical Anthropology*. (S18):186.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Sterling, P. and Eyer, J. 1988. Allostasis: A new paradigm to explain arousal pathology. In: S. Fisher and J. Reason, editors. *Handbook of Life Stress, Cognition and Health*. New York: John Wiley & Sons.

Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E. 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution of Human Behavior*. 21:79-95.

Strier, K.B. 1987. Activity budgets of woolly spider monkeys or muriquis *(Brachyteles arachnoides)*. *American Journal of Physical Anthropology*. 13:385-195.

Strier, K.B. and Ziegler, T.E. 2005. Advances in field-based studies of primate behavioral endocrinology. *American Journal of Primatology*. 67(1):1-4.

Strier, K.B., Ziegler, T.E., Wittwer, D.J. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis *(Brachyteles arachnoides)*. *Hormones and Behavior*. 35:125-134.

Struhsaker, T.T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Gainseville: University Press of Florida.

Tattersalll, I. 1987. Cathemeral activity in primates - a definition. *Folia Primatologica*. 49(3-4):200-202.

Tecot, S. 1999. *The effect of habitat on fecal cortisol concentrations in squirrel monkeys* (Saimiri sciureus) [Master's Thesis]. Austin: University of Texas at Austin.

Tecot, S. 2001. Field methods for collecting fecal cortisol: A test of four Malagasy primates. *American Journal of Primatology*. 54(S1):32-33.

Tecot, S. 2007a. Seasonality phenology and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology Suppl* S44:230.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Terborgh, J. 1986a. Community aspects of frugivory in tropical forests. In: A. Estrada and T.H. Fleming, editors. *Frugivores and Seed Dispersal*. Dordrecht: Dr. W. Junk Publishers. Pp. 372-384.

Terborgh, J. 1986b. Keystone plant resources in the tropical forest. In: M.E. Soulé, editor. *Conservation Biology, the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc. Pp. 330–344.

Terio, K.A., Citino, S.B., Brown, J.L. 1999. Fecal cortisol metabolite analysis for noninvasive monitoring of adrenocortical function in the cheetah *(Acinonyx jubatus)*. *Journal of Zoo and Wildlife Medicine*. 30(4):484-491.

Tilden, C.D. and Oftedal, O.T. 1995. The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: L Alterman, GA Doyle and MK Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 119-131.

Touma, C. and Palme, R. 2005. Measuring fecal glucocorticoid metabolites in mammals and birds: The importance of validation. *Annals of the New York Academy of Sciences*. 1046(1):54-74.

Touma, C., Palme, R., Sachser, N. 2004. Analyzing corticosterone metabolites in fecal samples of mice: a noninvasive technique to monitor stress hormones. *Hormones and Behavior*. 45(1):10-22.

Turk, D. 1995. *A Guide to the Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Turk, D. 1997. *A Guide to Trees of Eastern Madagascar and Ranomafana National Park*. Missouri Botanical Garden, St. Louis.

UNESCO. 2003. United Nations Educational Scientific and Cultural Organization World Heritage News.

van Horn, R.N. and Eaton, G.G. 1979. Reproductive physiology and behavior in prosimians. In: R. D. Martin, editor. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 79-122.

van Schaik, C., and van Noordwijk, MA. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques *(Macaca fascicularis)*. *Journal of Zoology*. 206:533-549.

van Schaik, C.P. and Pfannes, K.R. 2005. Tropical climates and phenology: a primate perspective. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 23-51.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs *(Varecia rubra)* on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. *American Journal of Primatology*. 66(4):393-394.

von der Ohe, C.G., Wasser, S.K., Hunt, K.E., Servheen, C. 2004. Factors associated with fecal glucocorticoids in Alaskan Brown bears *(Ursus arctos horribilis)*. *Physiological and Biochemical Zoology*. 77(2):313-320.

Walsberg, G.E. 2003. How useful is energy balance as an overall index of stress in animals? *Hormones and Behavior*. 43(1):16-17.

Wasser, S.K. 1996. Reproductive control in wild baboons measured by fecal steroids. *Biology of Reproduction*. 55(2):393-399.

Wasser, S.K., Bevis, K., King, G., Hanson, E. 1997. Noninvasive physiological measures of disturbance in the Northern Spotted Owl. *Conservation Biology*. 11(4):1019-1022.

Wasser, S.K. and Starling, A.K. 1988. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology*. 16(2):97-121.

Watson, S.L., Ward, J.P., Davis, K.B., Stavisky, R.C. 1999. Scent-marking and cortisol response in the small-eared bushbaby *(Otolemur garnettii)*. *Physiology and Behavior*. 66(4):695-699.

Wehr, A. 1998. Effect of seasonal changes in daylength on human neuroendocrine function. *Hormone Research*. 49(3-4):118-124.

Weinberg, C.R., Moledor, E., Baird, D.D. 1994. Is there a seasonal pattern in risk of early-pregnancy loss. *Epidemiology*. 5(5):484-489.

Weingrill, T., Gray, D.A., Barrett, L., Henzi, S.P. 2004. Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*. 45(4):259-269.

White, F., Overdorff, D.J., Balko, E., Wright, P.C. 1995. Distribution of ruffed lemurs *(Varecia variegata)* in Ranomafana National Park, Madagascar. *Folia Primatologica*. 64:124-131.

Whitten, P.L. and Brockman, D.K. 2001. Strepsirrhine Reproductive Ecology. In: P.T. Ellison, editor. *Reproductive ecology and human evolution*. New York: Aldine de Gruyter. Pp. 321-350.

Whitten, P.L., Brockman, D.K., Stavisky, R.C. 1998a. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*. Pp. 1-23.

Whitten, P.L., Stavisky, R., Aureli, F., Russell, E. 1998b. Response of fecal cortisol to stress in captive chimpanzees *(Pan troglodytes)*. *American Journal of Primatology*. 44(1):57-69.

Wiebe, R.H., Williams, L.E., Abee, C.R., Yeoman, R.R., Diamond, E.J. 1988. Seasonal changes in serum dehydroepiandrosterone, androstenedione, and testosterone levels in the squirrel monkey (*Saimiri boliviensis boliviensis*). *American Journal of Primatology*. 14(3):285-291.

Wikelski, M., Hau, M., Wingfield, J.C. 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology*. 81(9):2458-2472.

Wilson, M.I., Brown, G.M., Wilson, D. 1978. Annual and diurnal changes in plasma androgen and cortisol in adult male squirrel monkeys *(Saimiri sciureus)* studied longitudinally. *Acta Endocrinologica*. 87(2):424-433.

Wingfield, J.C. 2005. Flexibility in annual cycles of birds: implications for endocrine control mechanisms. *Journal of Ornithology*. V146(4):291-304.

Wingfield, J.C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G.S., Freed, L., Lepson, J. 1997. Environmental stress, field endocrinology, and conservation biology. In: JR Clemmons and R Buchholz, editors. *Behavioral Approaches to Conservation in the Wild* Cambridge: Cambridge University Press. Pp. 95-131.

Wingfield, J.C. and Sapolsky, R.M. 2003. Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*. 15(8):711-724.

Wright, P.C. 1992. Primate ecology, rainforest conservation and economic development: Building a national park in Madagascar. *Evolutionary Anthropology*. 1:25-33.

Wright, P.C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 16(5):835-854.

Wright, P.C. 1997. The future of biodiversity in Madagascar: A view from Ranomafana National Park. In: S. G. Goodman and B. D. Patterson, editor. *Natural Change and Human Impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press. Pp. 381-405.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*. 42:31-72.

Wright, P. and Andriamihaja, B. 2002. Making a Rain Forest National Park Work in Madagascar: Ranomafana National Park and Its Long-term Research Commitment. In: J. Terborgh, C. van Schaik, L. Davenport and M. Rao, editors. *Making Parks Work: Strategies for Preserving Tropical Nature*. Washington: Island Press. Pp. 112-136.

Young, A.L., Richard, A.F., Aiello, L.C. 1990. Female dominance and maternal investment in Strepsirhine primates. *American Naturalist*. 135:473-488.

Zav'yalov, E.L., Gerlinskaya, L.A., Evsikov, V.L. 2003. Estimation of stress level in the bank vole *Clethrionomys glareolus* (Rodentidae, Rodentia) by fecal corticosterone. *Zoologichesky Zhurnal*. 82(4):508-513.

Ziegler, T.E. 2000. Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*. 71:6-21.

Ziegler, T.E., Scheffler, G., Snowdon, C.T. 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*. 29(3):407-424.

Ziegler, T.E., Washabaugh, K.F., Snowdon, C.T. 2004. Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*. 45(2):84-92.

Ziegler, T.E., Wegner, F.H., Snowdon, C.T. 1996. Hormonal responses to parental and nonparental conditions in male cotton-top tamarins, *Saguinus oedipus*, a New World primate. *Hormones and Behavior*. 30(3):287-297.

Ziegler, T.E. and Wittwer, D.J. 2005. Fecal steroid research in the field and laboratory: Improved methods for storage, transport, processing, and analysis. *American Journal of Primatology*. 67(1):159-174.

Chapter 2: Environmental Seasonality: Seasonal Changes in Plant Phenology and Climate in Two Sites in Ranomafana National Park, Madagascar

INTRODUCTION

The physical structure, species composition, and phenological (reproductive) patterns of the flora in a habitat have profound consequences for sympatric organisms, and the physical habitat may be one of the strongest evolutionary forces experienced by any species. The structural characteristics and reproductive schedule of trees, for example, may impact not only an animal's direct nutrient intake, but also its range and route (Overdorff, 1993b; Cant *et al.,* 2001; Grassi, 2001; Di Fiore and Suarez, 2007), locomotion (Dagosto and Yamashita, 1998), safety from predators (Curtis *et al.,* 1999; Miller, 2002), and activity pattern (Curtis *et al.,* 1999), all of which are related to energy intake and expenditure and are thus potential contributors to the energetic balance of organisms. Ultimately, phenological cycles have important implications for animals' life history schedules. Life history theory predicts that reproduction and growth schedules are the result of adaptation to the limitations of a particular environment (Charnov, 1993), and these schedules afford animals the greatest likelihood of survival and reproduction in such an environment (Daan and Tinbergen, 1997). To maximize fitness animals should be keenly tuned to the rhythms of their environment.

Plant phenological events are also "integrative indicators" of season (Chen, 2003) since they are caused foremost by climate (Chen, 2003) (*e.g.,* moisture, photoperiod, temperature) and in turn impact the interaction of the participants of an ecosystem. Accordingly, plant phenology is also a common way to characterize a habitat and its

seasonality, and has been employed broadly in studies investigating the impact of resource availability upon primary consumers (van Schaik *et al.*, 1993; Wright, *et al.,* 2005; Wright, 2006).

With the advancement of non-invasive field endocrinological techniques (Risler *et al.,* 1987; Gross, 1991; Miller *et al.,* 1991; Monfort *et al.,* 1997; Whitten, *et al.,* 1998ab; Cavigelli, 1999; Stavisky *et al.*, 2001b) it becomes possible to investigate the direct impact of forest structure and resource availability on the physiology of primary consumers, and answer questions related to 'evolutionary ecology' (Whitten, 2000) such as what energetic strategies are selected for by particular environments. To date, ecological endocrinology studies are rare, and despite a recent desire to compare species in different habitats, none have employed a combination of rigorous, long-term measures of habitat structure, diversity, productivity, and climate concurrent with endocrinological measures. Often one discrete measure is made to characterize productivity in habitats (*e.g.,* DBH, Chapman *et al.,* 2006), seasons are broadly categorized as 'scarce/lean' or 'abundant', and habitats are classified as 'disturbed/fragmented' or 'undisturbed/continuous'. The goal of this chapter is to better understand the physical environments of two forests in southeastern Madagascar with variable histories of habitat disturbance, to ultimately provide deeper insight into the primary consumer-ecology relationship.

Community Relationships: Climate and Phenology

Phenological events are part of a plant's life history and are thus under natural selection to occur at the optimal time for a particular species in a particular environment (Begon *et al.,* 1990; Pianka, 1994). Phenological events are affected by natural resources such as sunlight, temperature, soil, and moisture (B. Johnson, 2002), and measuring the

dispersion of phenological events can reveal much about a community and the forces shaping it.

Rainfall is often regarded as one of the most important factors influencing the timing of phenological events (Sørg and Røhner, 1996; Morellato *et al.,* 2000), and positive relationships between fruiting and rainfall have been found (Atsalis, 1999aa; Hemingway, 1996; Sørg and Røhner, 1996; Chapman *et al.,* 1999). Though patchy in time and space, fruit may thus be a predictable resource insofar as its availability is cued by the climate in an environment.

Though rainfall and plant reproduction, specifically fruiting, are often assumed to be directly related, van Schaik and Pfannes (2005) conducted a meta-analysis of seasonal phenology in tropical and woodland primate habitats, and found that although flushing and flowering increased with rainfall seasonality, fruiting was not related to rainfall. These results raise the possibility that rare or low-quality food items may be more predictable food resources than high-quality fruits in seasonal environments, and the availability of fruit in the environment may be more randomly dispersed in relation to precipitation.

It is unclear why results from these studies differ, though van Schaik and Pfannes (2005) suggest that a positive relationship between rainfall and fruit may be present in fruit with high water content. Thus, the association between rainfall and fruiting may be variable. Further research is necessary to determine the nature of this relationship in specific habitats, as rainfall patterns have been used to characterize the predictability of food resources (*e.g.,* Dewar and Richard, 2007).

Community Relationships: Flora and Fauna

The structure, diversity, and productivity of a forest are inextricably linked with the behavior of primary consumers. Phenological events are impacted by dispersal and pollinating agents and plant predators (van Schaik *et al.,* 1993; Chapman *et al.,* 1999), which in turn influence seed dispersal and predator-avoidance (Begon *et al.,* 1990; Pianka, 1994). The relationship between flora and fauna is often symbiotic, and the physical environment depends in part upon the maintenance of this relationship. Our own reliance upon plant-pollinator relationships and the pollinator's role as "bioindicator" (Kevan, 1999) has recently been illuminated with the seemingly widespread disappearance of honeybees, or Colony Collapse Disorder (Berenbaum, 2007; Johnson, 2007). Despite the fact that the extent of Colony Collapse Disorder has yet to be assessed, or cases have yet to be confirmed, this phenomenon has the potential to eliminate an astounding 1/3 of agricultural crops in the United States (Berenbaum, 2007; Johnson, 2007). Several non-flying mammalian species (Sussman and Raven, 1978; Kress *et al.,* 1994; Carthew and Goldingay, 1997), including primates (Coe and Isaac, 1965; Martin, 1972; Hladik and Charles-Dominique, 1974; Sussman and Raven, 1978; Petter, 1978; Hladik, 1979; Prance, 1980; Janson *et al.,* 1981; Torres de Assumpção, 1981; Garber, 1988; Ferrari and Strier, 1992; Overdorff, 1992; Nilsson *et al.,* 1993; Kress *et al.*, 1994; Wright and Martin, 1995; Birkinshaw and Colquhoun, 1998), are suggested to be important pollinators as well, and many tropical forests depend upon the successful exploitation of foods from primary consumers (Sussman and Raven, 1978; Traveset, 1999; Di Fiore and Suarez, 2007).

It has been suggested that some primate species may even create their own ecosystems through coevolutionary processes (Di Fiore and Suarez, 2007). For example,

many primates are also known seed dispersers (Dew and Wright, 1998; Raju and Rao, 2006). Habitual use of paths to reach food sources by, for instance, woolly and spider monkeys in the New World (Di Fiore and Suarez, 2007), brown, red-bellied, and black and white ruffed lemurs in Madagascar (Dew and Wright, 1993), and bonnett macaques and langurs in India (Raju and Rao, 2006) results in defecation along those paths. As seed dispersers these species effectively plant their routes with new food sources over the course of several years. One of the implications of this relationship is that timber extraction and migration to new habitats with different vegetation (including variable habitat structure and phenological schedules) are likely more difficult for these primary consumers than currently appreciated; spatial and temporal predictability of food sources are decreased and energetic requirements may increase because their 'gardens' may no longer exist, and effective solutions to critical low resource seasons may be dangerously reduced. Thus, when elements of such tightly knit relationships are altered, the system is ripe for selection as organisms are required to adjust.

Energetic Balance in Seasonal Environments

The main challenge for primary consumers in acquiring and ingesting food is balancing energy expenditure with energy intake. To acquire sufficient nutrients and ensure that the energy spent searching for food will be replenished, animals may depend upon a level of resource predictability, selecting certain behavioral and dietary strategies based upon what is available, where it is available, and when it is available. For instance, ecologists often label certain times of the year 'lean seasons' because, although food may be available, it may be more distantly or sparsely located or poorer in nutritional quality than during other times of the year (van Schaik *et al.,* 1994). To accommodate the challenges inherent in acquiring distantly located and/or poor-quality foods, species must

store energy prior to the lean season (*e.g.,* Knott, 1998; Pereira *et al.,* 1999), and/or shift activity, ranges, or diets during the lean season. For instance, rufous lemurs *(Eulemur fulvus rufus)* exploited fewer, larger, uncommon, and more uniform patches, and even migrated for several months one year when food was scarce (Overdorff, 1996b). In any situation, storing energy or temporally modifying activity and diet should be evident in organisms subject to fluctuating food availability and shifting energetic requirements.

The cyclicity of resources in even tropical environments can have profound implications for primary consumers (Chivers, 1991). Despite behavioral modifications, seasonal disparities in the food supply, whether predictable or not, may cause periods of energetic challenge during food shortages. Some primate species experience decreased body condition during these times (Knott, 1998; Wikelski *et al.,* 2000; Lewis and Kappeler, 2005), and many suggest that low resource periods may be the most critical times for primates (Milton, 1982; Terborgh, 1983, 1986ab; Chapman and Chapman, 1999; Brugiere *et al.,* 2002), particularly frugivores. For instance, during years when important scarce season fruits are unavailable, ringtailed lemur (*Lemur catta*) infant and maternal mortality increased markedly (Sauther, 1998).

When a resource is predictably available during the lean season it may fulfill the requirements of a keystone resource (Leighton and Leighton, 1983; Terborgh, 1986b). For example, during critical times *Bakarella* (mistletoes) sustain mouse lemurs (*Microcebus rufus,* Atsalis, 1999aa) and sifaka (*Propithecus diadema,* Irwin, 2006) in altered forests where light gaps have encouraged the growth of this parasitic plant. In fact, sifaka in heavily degraded forest may rely upon this resource throughout the year (Irwin, 2006). *Ficus sp.* are the quintessential keystone resources, sustaining several tropical primate species (*e.g.,* Terborgh, 1983, 1986b; Estrada and Coates-Estrada, 1985;

but see Gautier-Hion and Michaloud, 1989). Several species appear to rely upon this resource in Madagascar (*e.g., Eulemur rubriventer* and *Eulemur fulvus rufus,* Overdorff, 1993ab; *Hapalemur griseus,* Grassi, 2001; *Eulemur fulvus rufus* x *Eulemur albocollaris* hybrids*,* S. Johnson, 2002). However, its low densities on the island, as well as in Gabon (Gautier-Hion and Michaloud, 1989), are proposed to be responsible for low vertebrate frugivore densities (Goodman and Ganzhorn, 1997), thus supporting Terborgh's (1986b) assertion that keystone resources may set the limits to a habitat's carrying capacity. In other words, the presence of particular food sources during the lean season may be the most critical in determining the behavior, life history, and success of primary consumers. A thorough understanding of the structure and phenology of the habitat will enhance investigations of the behavioral ecology of species, particularly those studies concerned with the flexibility potential of species.

The Impact of Selective Logging

Anthropogenic practices often change the face of an environment, as is abundantly clear throughout the world. While some excellent phenological and structural investigations have been conducted in altered forests (*e.g.,* Sørg and Røhner, 1996; Balko and Underwood, 2005; Irwin, 2006; Arrigo-Nelson, 2006; Riley, 2007), and trends in a forest's response to severe degradation have been illuminated, the phenological response to selective timber extraction and the resultant habitat structure is less clear (Bawa and Hadley, 1990). Logging may upset phenological cycles (Balko and Underwood, 2005), either exacerbating or reducing synchrony, but whether this is a benefit or detriment to primary consumers varies. Large gaps in the forest canopy enable light to reach the forest floor, and food production, quality, and diversity can actually increase with the removal of large trees (Ganzhorn, 1995b; Purvis and Hector, 2000), as exemplified by

Bakarella (see above) (Atsalis, 1999aa; Irwin, 2006). As Grassi (2001) notes, while such diversity may increase fruit quality, it is really the folivorous species which benefit from increased leaf quality in these areas (Ganzhorn, 1995b; Kowalewski and Zunino, 1999; Oates, 1996; Goldstein and Richard, 1989; Onderdonk and Chapman, 2000). Selective extraction often removes large fruiting trees on which frugivorous species depend (or have 'planted'), in effect reducing the number of patches per unit area. Frugivores do tend to be more sensitive to habitat modification (Johns and Skorupa, 1987; Marsh *et al.,* 1987; Richard and Sussman, 1987; Struhsaker, 1997; Harcourt, 1998) in part due to the distribution of fruiting resources and consequently their relatively large home range requirements (Terborgh, 1986a; Balko, 1998).

Forest dynamics resulting from selective harvesting play a role as well. For instance, while light gaps may increase plant species diversity, the extraction of specific species yields a forest with a different structure and species composition than natural processes, such as tree falls, do. Contrary to selective extraction, natural processes result in spatially *unpredictable* open spaces for recolonization (Phillips *et al.,* 1994). Consequently, the opportunity for large-scale competition, and therefore an invasive species to dominate an area, is decreased (Phillips *et al.,* 1994). More disturbed forests with spatially concentrated extraction are then more likely colonized by invasive species, and structural and species diversity may be reduced on a large spatial scale.

In general, a regenerating forest is typically composed of smaller and shorter trees, smaller fruit patches, and altered phenological cycles, resulting in resources with patchy distributions (Oates *et al.,* 1990; Ganzhorn, 1992, 1995b; Oates, 1996; Irwin, 2007) and overall less food than undisturbed forests (Riley, 2007). However, selective extraction may take on many forms. For instance, one or a few species may be largely or

completely eliminated, or a variety of species may be equally culled. Plant species diversity may be more (Ganzhorn, 1992; Oates, 1996) or less (Turner, 1996) diverse, depending in part upon the level of disturbance (see above; Connell, 1978). Resources may be patchy (Chapman, 1988) or uniformly available (Riley, 2007). A prime example of the uncertain habitat structure that selective extraction or minor logging may yield comes from Ranomafana, Madagascar. Ganzhorn and colleagues (2003) found that forest fragments in Ranomafana were comprised of either few individuals of several species (low abundance, high richness), or several individuals of few species (high abundance, low richness). Thus, in the latter case, if keystone resources are extracted, animals may be unable to survive critical low-resource periods (Terborgh, 1986b; Sauther, 1998), and may also benefit by having *more* resource options during periods of scarcity.

Madagascar

Climate and Phenology

Madagascar is suggested to differ from other primate habitats (Wright, 1999; Wright *et al.,* 2005; see Janson and Verdolin, 2005) because of extremely unpredictable rainfall patterns which result in unpredictable fruiting patterns (Dewar and Richard, 2007). Rainfall varies both intra- and inter-annually to a much greater extent than in other areas of the world (Dewar and Richard, 2007). Phenological cycles are unpredictable and asynchronous, with long periodicity and irregularity (Ganzhorn, 1995b; Hemingway, 1995; Hemingway and Overdorff, 1995; Overdorff, 1996b; Balko, 1998; Wright, 1999; Bollen and Donati, 2005; Balko and Underwood, 2005; Wright *et al.,* 2005), particularly in the eastern rain forests (Ganzhorn *et al.,* 1999a). For instance,

fruit scarcity may last as long as six months, three months longer than in other primate habitats (Wright, 1999; Wright *et al.,* 2005).

Though a positive relationship between rainfall and fruiting was reported in Ranomafana National Park in southeastern Madagascar (Hemingway, 1996; Grassi, 2001), other studies found that fruit production in Ranomafana was not related to rainfall (Hemingway, 1998). Overdorff and Wright (unpublished manuscript) report that phenological cycles are inconsistently related to rainfall, with no clear relationship in some years and strong relationships in other years, possibly explaining disagreement among studies. This variability in the relationship between rainfall and fruiting, superimposed upon extremely unpredictable rainfall patterns (Dewar and Richard, 2007), may generate particularly complex plant-consumer relationships. Furthermore, Bollen and Donati (2005) report that fruiting, flowering, and flushing occur close in time in many of the rainforests in Madagascar, resulting in little compensation for fruit scarcity during the lean season.

Particularly long low resource periods and unreliable periods of potential energetic storage may present fauna in these forests with a strikingly challenging environment within which to find food, reproduce, and survive. Moreover, Madagascar is subject to habitat alteration in the form of extreme, potentially destructive weather (Ganzhorn, 1995a; Wright, 1999; Jury, 2003), and relatively recent and extensive habitat disturbance (Dufils, 2003).

Habitat Change in Madagascar

Weather

Habitat alteration can take many forms, and in Madagascar, the only location inhabited by lemurs, these include both natural and anthropogenic disturbances. Because of its position on the globe (10˚-20˚ latitude, in the cyclone belt), Madagascar is a magnet for cyclone activity during the austral summer (approximately 10 tropical cyclones per year) (Ganzhorn, 1995a; Wright, 1999; Jury, 2003). During this past 2006-2007 cyclone season Madagascar was battered by a total of seven cyclones which devastated the island and severely affected an estimated 126,000 people (Swarup, 2007) in an already poverty-stricken nation (ranked 143rd in development, of 177 countries, UNDP, 2006). A cyclone's impact on a forest may be complex. Flooding and landslides may result from heavy rains, and vegetative stripping or complete uprooting of trees may result from staggeringly fast winds (Donque, 1972; Ganzhorn, 1995a; Wright, 1999; Ratsimbazafy, 2006) with canopy tree losses of 85% reported (Ratsimbazafy, 2006). Ratsimbazafy (2006) observed the impact of cyclone Gretelle in 1997 and was able to assess the effect of the cyclone upon plant species composition. Many species specialize in exploiting disturbed areas, and he reported that more than 40% of the Manombo forest has since been colonized by alien plant species since Gretelle's impact, jeopardizing the original plant community. In the end this translates to a drastic reduction in available foods for animals to exploit (a 70% reduction in fruiting plants) (Ratsimbazafy, 2006) and a reduction in the number and diversity of resources "planted" by seed dispersers. An associated reduction in faunal body weights (Ratsimbazafy, 2002) and population densities (Wright, 1999) may occur as well. Cyclones are just one form of natural disaster that Madagascar is faced with on an annual basis; environmental stochasticity is varied and common, and only one category of habitat alteration in this country.

Anthropogenic Change

The evergreen forests of Madagascar experience a reported 102,000 ha/yr loss (Dufils, 2003). Ranomafana National Park, Madagascar is a good example of a habitat which has been altered through a variety of natural and anthropogenic forces. According to Dufils (2003; data from ANGAP), Ranomafana National Park has a mean annual deforestation rate of 1.15% despite being one of the most successful national parks in the world. In addition to the effects of weather, this area has been impacted in several ways, such as through resource extraction from timber concessions granted prior to the establishment of this area as a national park in 1991 (Wright, 1992, 1997; Peters, 1999; Wright and Andriamihaja, 2002), tree felling by locals for items such as honey (Tecot, personal observation), clearing of areas for settlement in the 1940s (Wright, 1997), and the use of forest products for items such as baskets or food such as crayfish (though extraction of most crayfish species has been shown to be sustainable) (Peters, 1999; Jones *et al.*, 2005). Edge effects are also apparent as the result of deforestation for agriculture outside park boundaries (Ramaharitra, 2006). Studies in Ranomafana National Park determined that disturbed areas have been recolonized by secondary growth consisting of both native and exotic species (Turk, 1995; Durham, 2003). Selective logging has resulted in altered forest structure, species (plant and lemur) composition, and food availability for several species (White *et al.,* 1995; Balko, 1998; Dagosto and Yamashita, 1998; Grassi, 1998; Balko and Underwood, 2005; Arrigo-Nelson, 2006). When already poor quality environments undergo food declines, energy requirements for primary consumers may be even higher than in healthy environments, and energy deficits may be exacerbated or prolonged during these critical times.

Lemurs

Many primate species are able to survive food declines, or nutrient-poor or edge environments, by changing their behaviors or diversifying their diets accordingly (*e.g., Alouatta:* Glander, 1981, Chapman, 1987, Estrada *et al.,* 1999; *Callithrix:* Passamini, 1998; *Colobus:* Dasilva, 1992; *Macaca:* Tsuji *et al.,* 2006, Riley, 2007; *Saimiri:* Boinski, 1987; *Tarsius:* Gursky, 2000). Lemurs are no exception (*e.g., Eulemur:* Overdorff, 1993ab, 1996ab; *Hapalemur:* Grassi, 2001; *Lemur:* Rasamimanana and Rafidinarivo, 1993; *Microcebus:* Atsalis, 1999aa; *Propithecus:* Richard, 1978, Hemingway, 1995, Hemingway and Bynum, 2005, Irwin, 2006, 2007; *Varecia*: Balko, 1998), for example adopting strategies such as torpor (Wright & Martin, 1995, Schmid & Kappeler, 1998) or migration (Overdorff, 1996b) during food decline, or modifying time budgets in degraded areas (Arrigo-Nelson, 2006; Irwin, 2006).

Lemurs in particular are important pollinators and seed dispersers (Overdorff, 1992; Dew and Wright, 1993; Kress *et al.,* 1994; Carthew and Goldingay, 1997), with strong evidence supporting an ancient relationship in Madagascar (Kress *et al.,* 1994). It remains to be determined whether seasonal behavioral changes are stable strategies which help species avoid the stress of food scarcity, or the result of an inability to acquire sufficient energy and thus an indication of stress. Are behavioral modifications sufficient to overcome periods when resources are scarce, or are these risky times and risky habitats?

Furthermore, lemur behavior is strongly bound to the vegetation in their habitats and they may be heavily influenced by habitat change affecting the structure and diversity of plants and the availability of food sources in the habitat. Yet it is unknown whether lemurs truly cope when scarce periods are intensified, such as in disturbed habitats, or whether they undergo chronic stress.

Goals

The goal of this chapter is to better understand the physical environments of two forests in southeastern Madagascar inhabited by *Eulemur rubriventer* with variable histories of habitat disturbance, to ultimately provide deeper insight into the primary consumer-ecology relationship. Given the inconsistent climate and phenological patterns from year to year in Madagascar, this study expands the long-term database of the physical structure and phenological patterns of vegetation in Madagascar in general, and the rain forests of Ranomafana National Park in particular (Overdorff, 1991; Meyers and Wright, 1993; Turk, 1995; Balko, 1998; Hemingway, 1998; Atsalis, 1998; Hemingway and Overdorff, 1999; Tan, 2000; Grassi, 2001; Durham, 2003; Brown and Gurevitch, 2004; Balko and Underwood, 2005; Arrigo-Nelson, 2006), by sampling microhabitats previously unstudied in two habitats concurrently. As part of a longitudinal study in Ranomafana National Park, this study further enables investigation of the dynamics of forest regeneration after selective extraction.

Simultaneous sampling in two sites enables investigations of the flexibility of primary consumers, which are essential for a complete understanding of the behavioral ecology of species as well as for evaluating the success of coping mechanisms. Comparisons of two structurally diverse forests inhabited by a lemur species can facilitate such an analysis to the extent that the forest structure and phenological patterns associated with the species' seasonal behavioral and physiological changes can be observed.

Specifically, this study characterizes the forest structure in each site, documents seasonal changes in the environment, and investigates the relationship between climate and plant phenology. Community and population level habitat structure are determined

by identifying and assessing tree species present in botanical plots, and productivity is calculated using measures of species' relative dominance, abundance, diversity, and synchrony. Subsequently, climate and phenological seasons are established by determining periods of peak production. These elements are then compared across sites over a nineteen month period to quantify habitat differences.

Hypotheses and Predictions

Based upon previous research at these sites, the following general hypotheses were made:

The first null hypothesis states that forest quality does not differ between plant communities, and predicts that measures of forest production and habitat structure are not significantly different among sites with different levels of habitat disturbance. Balko and Underwood (2005) found that "the *impact* of selective logging is roughly equivalent to a removal rate that is 10 times greater than the actual number of harvested stems" (64) and a change in the spatial dispersion of trees may cause rapid crown expansion by trees adjacent to newly created gaps. Thus selective harvesting may alter the structure of a logged habitat substantially greater than the removal of selected tree species. Thus, timber extraction is alternatively hypothesized to have differentially impacted the forest quality of these plant communities, and forest quality is predicted to be higher in areas with less habitat disturbance.

The second null hypothesis states that weather is random and temperature and rainfall seasons are not apparent, and predicts that no significant differences in monthly rainfall or temperature will occur throughout the study. Eastern Madagascar does not experience a clearly delineated dry season (Hemingway, 1998; Britt, 2000; Bollen and

Donati, 2005), and temperature fluctuations in tropical forests are small. However, tropical forests may actually be quite seasonal (Terborgh, 1983, 1986b; van Schaik and Pfannes, 2005). In fact, several tropical mammalian species shift daily activity rhythm (the distribution of activities throughout the day) either to stay warm or cool as ambient temperatures and rainfall fluctuate (*e.g.,* Curtis *et al.*, 1999; Vasey, 2005; reviewed in Curtis & Rasmussen, 2002), speaking to the impact that these changes, however subtle, may have. Thus, temperature and rainfall are alternatively hypothesized to fluctuate predictably throughout the year**,** and clear wet/dry seasons and cool/warm seasons are predicted to occur. No site differences are predicted due to their close proximity.

The third null hypothesis states that phenological cycling is random (no phenological event can predict another phenological event) and seasonal productivity is not apparent. The temporal dispersion of phenological events is predicted to be random, with no indication of peaks (synchrony) in leaf flushing, fruiting, and flowering. Sites will be equally unpredictable, with few seasonally productive species. Furthermore, as one goal of this study is to determine how site differences impact primary consumers, the dispersion of phenological events in species exploited by *Eulemur rubriventer,* a representative primary consumer, will not differ from the site-wide pattern.

Phenological cycles are unpredictable and asynchronous, with long periodicity and irregularity (Ganzhorn, 1995b; Hemingway, 1995; Hemingway and Overdorff, 1995; Overdorff, 1996b; Balko, 1998; Wright, 1999; Bollen and Donati, 2005; Balko and Underwood, 2005), and fruiting in the eastern rain forests is even less predictable than in Madagascar's dry forests (Ganzhorn *et al.,* 1999a). However, inter-annual unpredictability in plant production, related in part to climatic stochasticity, does not preclude seasonality (Chapman *et al.,* 1999). Thus, phenological cycling is alternatively

hypothesized to be largely seasonal, and clear scarce and abundant fruit availability seasons are predicted to occur.

The more disturbed site is predicted to be less predictable with less seasonally productive species and high variation in food availability from month to month, and brief peaks and prolonged troughs in food availability. As trees with larger diameter at breast height (DBH) are preferred by many frugivorous species, such as *Eulemur rubriventer* (Overdorff, 1991; Durham, 2003; Tecot, this study), and larger trees were predicted to occur at the undisturbed site as a measure of forest quality (see above), the inter-site disparity in the productivity of species is hypothesized to be intensified in exploited species. Exploited trees in the more disturbed site are predicted to be less predictable and less seasonally productive than those in the undisturbed site.

The fourth null hypothesis states that phenological cycling is not constrained by climate. No significant relationships are predicted to exist between phenology and the climate variables temperature and rainfall, and these relationships are predicted to be equally weak in each site. Alternatively, phenological cycling is hypothesized to be influenced by climate because of the long evolutionary history of the vegetation in this environment**,** and phenology is predicted to be significantly correlated with temperature and rainfall. The relationships between fruiting, flowering, and flushing and climate are predicted to be weaker in the disturbed site because of the shorter evolutionary history of some plant species at that site.

METHODS

Research Sites

To characterize and compare the communities inhabited by *Eulemur rubriventer*, data were collected from Talatakely and Vatoharanana, two adjacent sites in Ranomafana National Park (RNP), Madagascar (Figure 2.1). These sites were ideal for this study because they are subject to similar climates but varying levels of habitat alteration. Controlling for climate, the effects of habitat quality can be assessed more readily and further enable the analysis of intra-specific cross-site behavioral differences. Furthermore, due to high site fidelity throughout a lifetime in *Eulemur rubriventer* (Overdorff and Tecot, 2006), these sites were sufficiently distant to represent two functionally separate entities. As a result of selective logging (Wright and Andriamihaja, 2002), the density and abundance of plant species differed significantly between the sites one decade ago (Turk, 1995; Wright, 1995; Balko, 1998). Though it is currently unknown if these forests differ in any significant way, the presence of lemur species varies among sites (Balko and Underwood, 2005; Tecot, personal observation).

RNP consists of approximately 43,500 ha of evergreen rain forest in Fianarantsoa Province, southeast Madagascar (between 21˚02' to 21˚25' S and 47˚18' to 47˚37' E) (Figure 2.1) (DuPuy and Moat, 1995). It is located along the eastern north-south escarpment which causes trade winds to rise and maintains humidity (90%) and moisture (B. Johnson, 2002; DuPuy and Moat, 2003). This park contains the largest known population of *Eulemur rubriventer* (Wright 1992), as well as at least 11 other primate taxa (Wright, 1992). RNP ranges from lowland forest (500m) to montane rain forest (1500 m), with low soil productivity (B. Johnson, 2002). This area can be highly seasonal with distinct wet and cool/dry seasons (Jury, 2003), and may experience large

peaks and prolonged troughs in food availability, particularly fruit (Hemingway, 1995; Morland, 1991; Overdorff, 1993a, 1996a; Overdorff and Strait, 1998). Mapped on this seasonal environment is inter-annual unpredictability. There is extreme variation in the amount of rainfall (avg. 1500 mm – 4000 mm per year), the lengths of wet and dry seasons (Overdorff and Wright, unpublished manuscript; Wright 1992), and annual phenological patterns from year to year (Overdorff, 1993a; Wright, 1999, 2006). Cyclone activity typically occurs January through March. The current study documents forest structure and biotic and abiotic patterns from September 2003 through March 2005.

Talatakely: At 500m in altitude, this site was heavily logged from 1986 to 1989 when approximately 5,600 ha of timber concessions were granted, and it is currently regenerating (Wright, 1992, 1997; Wright and Andriamihaja, 2002). In fact, the black and white ruffed lemur *(Varecia variegata variegata),* who was restricted to primary forest (Balko, 1998) and was absent from this site, has recently been making forays into Talatakely (Tecot, personal observation). As a result of habitat alteration, this site has been characterized as secondary rain forest with emergent *Eucalyptus* trees (Overdorff, 1988), with an understory largely consisting of Rubiaceae and Myrsinaceae, bamboo, and epiphytic species (Turk, 1995). Large stands of Chinese guava (*Psidium cattleianum*) have developed since the 1950s and comprise approximately 10% of the trail system (P. Wright, personal communication). Although this species is competitive and invasive, it has not aggressively spread over the course of the past 20 years (P. Wright, pers. comm.).

Vatoharanana: This site is located 6 kilometers south of Talatakely, at approximately 1200m in altitude. Although this site was selectively logged and approximately 1,000 trees were extracted (Wright, 1992, 1997; Balko, 1998; Wright and

Andriamihaja, 2002; Balko and Underwood, 2005), it is characterized by continuous primary forest with steep mountain slopes (Overdorff, 1988; White *et al.*, 1995; Balko, 1998; Dagosto and Yamashita, 1998; Grassi, 2001).

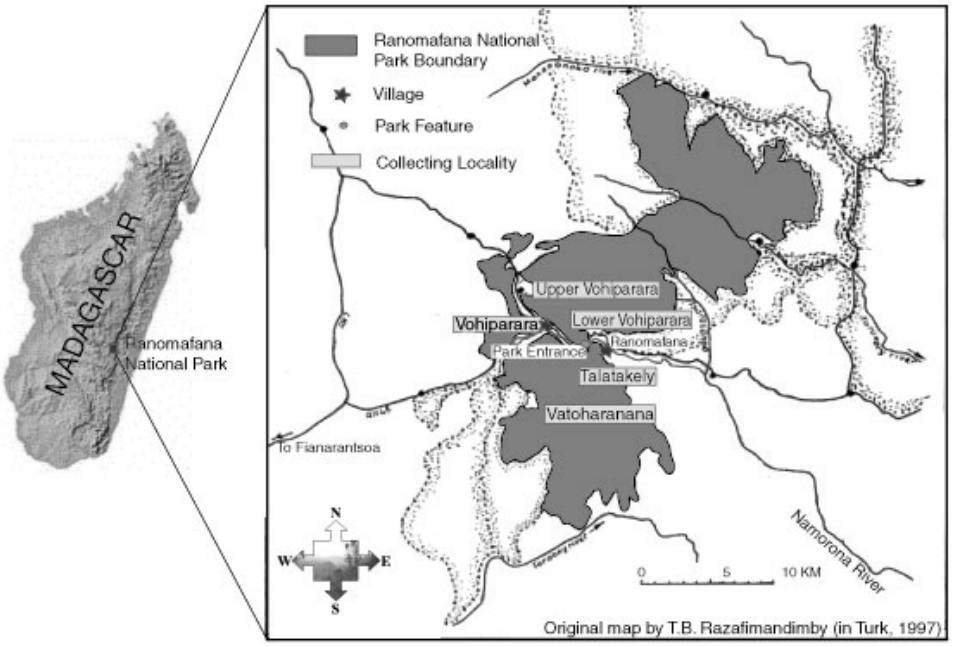


Figure 2.1. Map of Ranomafana National Park, Madagascar. Map from Turk (1997), modified by Elsom (2002). Printed with permission from E. Cunningham (formerly Elsom), CalAcademy.

Establishment of Botanical Plots

Three botanical plots were established in September 2003 at each site within known home ranges of *Eulemur rubriventer* for a total of six plots and 1473 plants (n_{Tala}=896; n_{Vato}=599). As plots of different dimensions but similar areas can give different density estimates (Ganzhorn, 2003), plots of the same dimensions (100m x 10m, 5m x 50m, 10m x 25m) were established at each site. Although Ganzhorn (2003) suggests that using 5-10 plots when sampling trees larger than 3-4 meters is ideal, the limitations imposed by the behavioral sampling regime reduced the amount of trees that

could be sampled monthly, and instead large plots of varying sizes were used. Each site contained botanical plots located on a highland ridge, a slope, and a valley.

To characterize each site and facilitate site comparisons, all lianas and trees $\geq$ 2.5 cm diameter at breast height (DBH) were identified by vernacular name, assigned numbers and marked with flagging tape or aluminum tags. While other studies in Ranomafana have recorded the phenology of all trees $\geq$ 5 cm (*e.g.,* Hemingway, 1998) or 10 cm (*e.g.,* Balko and Underwood, 2005) DBH, 2.5 cm was chosen as the minimum DBH for this study in order to capture the phenology of an important dietary item, *Psidium cattleianum* (guava) in the sample.

Data on DBH (cm), tree height (m), crown diameter (m; horizontal distance across the tree crown), crown depth (m; distance from the lowest branch to the top of the tree crown), and crown shape were recorded (although crown shape was not used in this analysis) with the help of research technicians. DBH, a reliable measure which may also indicate height, biomass, and age of the tree (Hladik, 1980; Chapman *et al.,* 1992) was measured with a DBH tape at approximately 1.3 m from the ground (Ganzhorn, 2003), using the lowest point if on a slope. Heights and crown sizes were visually estimated in meters. Subsequent to constructing plots, species designations were determined using published work by Overdorff (1991), Turk (1995), Schatz (2001), and the Missouri Botanical Garden database, and species inventories were compiled.

Forest Composition and Quality

Habitat Structure

Species richness, abundance, and basal area were calculated and measures of relative dominance, relative abundance, structural and species diversity, and evenness

were derived to further characterize each habitat. Species abundance was reported as the total number of individuals of each species in each community. Relative abundance (RA) was calculated for each taxonomic level as the proportion of all trees belonging to each family, genus, or species, multiplied by 100. Species richness is a commonly used numerical measure of the biological diversity of an area (Purvis and Hector, 2000; Kéry and Schmid, 2006) and was measured as the total number of species in each community. Because classifying Malagasy plant species identified by their vernacular names is particularly taxing, and because these designations are not as reliable as family and genus designations (Dorr, 2003), richness is also reported on the familial and generic levels for each botanical plot.

Forest Production

Basal area is a measure of forest biomass (Singh and Singh, 1991; S. Johnson, 2002) and, despite the exclusion of measures of crown or crop size, may be an indirect, reliable measure of tree cover (Cade, 1997) and forest production (Singh and Singh, 1991). Basal area is the cross-sectional area of the tree at breast height and was calculated as:

$$\pi\left(\frac{dbh(cm)}{2x100}\right)^2$$

Basal area (m^2) was calculated for each living tree in each plot and converted to total basal area per hectare. Basal area/ha was calculated for each plot and each site in total, and again for all stems in each of two categories: $\geq$ 10cm DBH and <10 cm DBH for each plot. Basal area was then used to determine relative dominance (RD) (after Balko, 1998 and Balko and Underwood, 2005; Atsalis, 1999aa), which was calculated for each family, genus, and species as:

RD = (sum of basal area of a species / total basal area) * 100

Relative dominance was viewed in relation to relative abundance (RD/RA; see below) to provide a description of the size distribution of trees at each site (Balko and Underwood, 2005).

Biological Diversity: Species and Structural Diversity Indices

As no single diversity measure is completely suitable for all questions (Purvis and Hector, 2000; Rennolls and Laumonier, 2000), species and structural diversity were measured in two ways: using the Shannon & Wiener Index (see Spellerberg and Fedor, 2003; Shannon and Weaver, 1963; Krebs, 1999) and Simpson's Diversity Index (Simpson, 1949). The Shannon & Wiener Index accounts for both species richness and evenness, where a higher index indicates greater diversity, specifically greater species/structure distinctiveness (number of species or structures) and/or evenness (numerically similar representation of species or structures) in the community. Diversity (H′) is defined as follows:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where S is the number of species (species richness) or structural categories present in the community, and p_i is the relative abundance of each *i*th species or structure. Relative abundance is defined as n_i/N, where n_i is equal to the abundance of each *i*th species or structure category and N is the total number of species or structures in the community.

Since the Shannon & Wiener Index is influenced relatively more by species richness than species evenness (almost twice as much as Simpson's Diversity Index), and since Simpson's Diversity Index is more influenced by species evenness than species richness (deJong, 1975), both indices were used in this study to yield a more comprehensive indication of diversity. Simpson's Diversity Index (D) is calculated as:

$$\mathbf{D = 1-\sum_{i=1}^{S} \frac{n_i(n_i-1)}{N(N-1)}}$$

where S is the number of species, n_i is the total number of individuals of the *i*th species, and N is the total number of individuals of all species in the community. Both indices range from 0 to 1 and represent the increasing probability that any two randomly chosen individuals will belong to the same species; higher scores represent greater diversity.

Species evenness (E) is a measure of the numerical similarity of species abundance in a community, providing some context for species richness by conveying how many individuals of each species are present in each community. This differs from relative species abundance because it presents a score for the entire site, and may be derived from the Shannon & Wiener Index. Species evenness is measured as E = H/ln(S), where H is the Shannon & Wiener index and S is species richness (Whittaker, 1972). Evenness has a minimum score of 0, indicating greatest variation between species, and a maximum score of 1, indicating least variation, or similar numbers of individual trees of all species; as the score decreases there is less consistency between species in the number of representative individuals in the community (i.e., several individuals of species X and few individuals of species Y).

Forest Composition and Quality Datasets

Two sets of data were used for inter-site analyses: (1) all trees $\geq$ 2.5cm DBH and (2) all trees $\geq$ 10cm DBH. The first dataset comprises all tagged trees in the study; the second dataset was used for consistency across studies (*e.g.,* Ganzhorn *et al.,* 1997; Balko, 1998; S. Johnson, 2002; Overdorff and Wright, unpublished manuscript), and was referred to as Subset 2. Structural diversity was determined only for Subset 2 and each tree was assigned a size category according to DBH in 5 cm increments from 10 cm DBH to 30 cm DBH (Ganzhorn *et al.,* 1997).

Seasonality

Climate

To determine seasons and investigate weather patterns, daily measurements of temperature and rainfall were recorded at each site throughout the study. Minimum and maximum temperatures were recorded in degrees Celsius each morning. Rainfall was collected in an open area with a rain gauge and measured in millimeters each morning, or in the case of high rain volume, when full throughout the day.

Daily minimum and maximum temperatures were averaged to yield daily means for each site individually and combined. Daily rainfall and temperature measures were averaged to yield weekly means, and weekly means were averaged in turn to yield monthly means. If one week spanned two months, the mean weekly value was assigned to the month encompassing the majority of those days. Where rainfall was unrecorded, the total rainfall for the month was divided by the number of days data were recorded, then multiplied by the total number of days in the month, for an estimate of monthly total rainfall. On days when data were unrecorded, data for Talatakely were supplemented with data collected by the Association Nationale pour la Gestion des Aires Protégées (ANGAP). Data were collected beginning September 2003 in Vatoharanana and October 2003 in Talatakely. Data collection terminated March 19, 2005. Wet seasons consisted of months in which rainfall exceeded 300mm. Warm seasons consisted of months in which the mean temperature exceeded 19˚ Celsius. The relationship between climate measures and fruiting phenology was also investigated.

Phenological Sampling

To document habitat quality, seasonal plant productivity, diversity, and food availability, and compare these parameters among sites, indices of plant phenology were

collected from all marked trees and lianas in each botanical plot in each site once per month according to the methods in Overdorff (1996b). Initially each liana and tree was assigned a number and flagged with flagging tape to facilitate monthly assessments. Data on the availability of fruits (ripe, unripe), flowers (buds, blooms), and leaves (immature, mature) on each identified tree and liana were recorded on a scale of 0 (absent) to 5 (full abundance) each month (Oates, 1977; Overdorff, 1996b). If a ranking of at least 1 was assigned, the food item for that individual tree was considered present. Data were collected on fruits, flowers, and leaves during the final week of each month from September 2003 through March 2005 over the course of two days. Mature leaves were abundant throughout the year so were not used to show fluctuations in food availability. Due to tree death and human error (i.e., inconsistent liana sampling), the number of plants sampled each month varied (Table 2.1). As a result of this variance from month to month, all data were converted to percentages for analysis.

Phenological Seasons

Food availability seasons and plant production were determined by totaling the number of trees and lianas with a score of 1-5 for each food item in each phenological development stage, and dividing by the total number of trees and lianas assessed each month in each site. This indicated presence or absence of each plant part in each stage, which is highly correlated with data weighted by DBH, abundance score, crown volume, or other measures commonly employed to measure the abundance of food items (Chapman *et al.,* 1994; Ganzhorn, 2003). For ease of comparison with other studies (*e.g.,* Atsalis, 1998; Hemingway, 1998), including long-term studies in Ranomafana (Wright *et al.,* 2005; Overdorff and Wright, unpublished manuscript), percentages were reported as indicators of monthly food availability in this study.

Since the dispersion, or synchrony, of one phenological event (*e.g.,* fruiting) may be impacted by the synchrony of other phenological events (flushing, flowering) (Gorchav, 1990), this study investigated the synchrony of all three stages to determine the seasonality of productivity in each site. The coefficient of dispersion (CD) (Sokal and Rohlf, 1995) was calculated to determine the synchrony of phenological phases in the plant communities present at each site (Chapman *et al.,* 1999; S. Johnson, 2002). For species-specific synchrony, the number of trees experiencing a phenological event was calculated for every identified species each month. CD was calculated as sample variance/mean for the number of monthly phenological events per species, including only those species for which more than one individual was present. This measure considers both the density and distribution of species (Goldsmith, 1999) and may indicate whether the presence of each food type is seasonally available or not. Species-specific and site-specific CDs for leaf flushing, fruiting, and flowering were determined. A random temporal distribution is indicated by a score of 1, and indicates unpredictability (one event does not affect the probability of another event); a clumped distribution is indicated by a score greater than 1 and may indicate a seasonal environment; and uniformity is indicated by a score lower than 1, and may indicate selection against seasonality. The index of dispersion (I_D = sample variance x df / mean) was used to determine significant departure from a Poisson distribution (Southwood, 1978).

Table 2.1. Number of trees and lianas in botanical plots sampled each month in each site are listed. The greater number of trees sampled in Talatakely is indicative of the higher density of trees in that site. All trees 2.5cm DBH and higher were included.

Month	Vatoharanana	Talatakely	Total
1	580	847	1,427
2	571	865	1,436
3	572	853	1,425
4	547	868	1,415
5	535	866	1,401
6	536	860	1,396
7	543	860	1,403
8	571	829	1,400
9	574	828	1,402
10	570	958	1,528
11	579	930	1,509
12	583	881	1,464
13	585	878	1,463
14	587	865	1,452
15	553	871	1,424
Mean	**565.73**	**870.60**	**1436.33**
Std. dev.	**18.00**	**33.87**	**40.28**
Total	**8,486**	**13,059**	**21,545**

Seasonality Datasets

For finer analyses of food availability (as suggested by Hemingway and Overdorff, 1999), a subset of the habitat assessment database was created. This dataset (referred to as Dataset 2) included only phenological data collected from botanical plots on plant species which *Eulemur rubriventer* were observed exploiting during behavioral observations. 633 individuals from 68 species and 31 families exploited by *E. rubriventer* were represented in Talatakely botanical plots and 422 individuals from 76 species and 33 families exploited by *E. rubriventer* were represented in Vatoharanana botanical plots. However, not all *E. rubriventer* food species were represented (see Appendices 1 and 2 for a list of all observed *E. rubriventer* foods by site).

Data Analysis

Data were analyzed overall and by site. Seasons were determined by (a) temperature, (b) rainfall, and (c) fruit availability. Nonparametric Spearman's rank correlation was used to analyze the relationship between rainfall and temperature. Kruskall Wallis tests for independence and ANOVAs were used to analyze inter- and intra-site differences in DBH, tree height, crown diameter, crown depth, and basal area. Pairwise comparisons of each parameter among botanical plots within each site were conducting using Mann-Whitney U tests. To assess the relationship between phenology and climate, monthly means were standardized and 2-tailed Pearson's correlations were run. In all cases, significance was set at $p \leq 0.05$.

RESULTS

Botanical Plots

Forest population and community structure

Structural characteristics of each site are summarized in Table 2.2. More than twice as many emergent trees ($\geq$ 30 cm DBH) were present in Vatoharanana (n = 40) than Talatakely (n = 17). Talatakely trees were on average 12% shorter (z = 1.644, $p<.01$) and diameter at breast height was on average 63% of the DBH of trees in Vatoharanana (z = 4.076, $p<.001$). There were significant differences in crown depth (z = 1.811, $p<.01$), but not crown diameter (z = 0.481, $p=.975$ ns), between sites. Basal area differed significantly between sites with Vatoharanana having larger forest biomass (z = 4.084, $p<.001$), and a very slightly lower coefficient of variation (CV Vato: 0.326; Tala: 0.329), implying a more uniform distribution of individual trees (Sagar and Singh, 2006).

Microhabitat differences were found within each community using Kruskall Wallis tests for differences between plots. In Talatakely significant differences in tree height ($X^2(2, n = 886) = 9.418$, $p<.01$), DBH ($X^2(2,n = 873) = 32.710$, $p<.001$), crown diameter ($X^2 (2, n = 886) = 13.006$, $p<.001$), and crown depth ($X^2 (2, n = 887) = 16.440$, $p<.001$) were found among plots (Figure 2.2). In Vatoharanana significant differences in height ($X^2(2, n = 542) = 6.413$, $p<.05$), DBH ($X^2(2, n = 539) = 16.937$, $p<.001$), crown diameter ($X^2(2, n = 542) = 15.785$, $p<.001$), and crown depth ($X^2(2, n = 542) = 23.369$, $p<.001$) were found among plots. Post-hoc Mann-Whitney U tests determined significant differences between each plot dyad. In Vatoharanana, significant differences were all with plot 1, the largest plot. In Talatakely, significant differences occurred between all plots (Figure 2.2).

Analyses were also performed on a subset of trees > 10cm DBH for comparison with other studies (e.g., Balko, 1998; Overdorff, 1991; Ganzhorn *et al.*, 1997; S. Johnson, 2002; Balko and Underwood, 2005), and to remove the bias of a large sample of guava in Talatakely. Trees in Vatoharanana (n = 185) remained significantly taller ($z = 3.018$, $p<.001$) than those in Talatakely (n = 149), although differences in DBH only approached significance ($z = 1.349$, p=0.052 ns; $M_{Vato} = 22.45$; $M_{Tala} = 18.37$). Mean basal area of trees 10cm DBH and larger also did not differ significantly between sites ($z = 1.105$, p=0.174 ns), nor did total basal area/ha ($z = -1.528$, p=0.13 ns), though these measures were higher in Vatoharanana (Table 2.3). Crown depth remained significant ($z = 1.442$, $P<.05$) and crown diameter became significantly different ($z = 1.922$, $p<.001$) across sites. Thus it appears that current DBH differences between sites are mainly due to the larger number of small trees in Talatakely, and height differences are due to the larger number of tall trees in Vatoharanana.

Forest population and community diversity: taxonomic composition

Overall: All tagged trees and lianas in the six plots represented a minimum of 49 families; 31 individuals were unidentified at the family level. 16 families were rare (represented by 5 or fewer individuals, after Chapman *et al.,* 1999). The 5 rarest families, only represented by a single tree, were Connaraceae, Icacinaceae, Menispermaceae, Rhamnaceae, and Schizeaceae. The six most relatively abundant families combined accounted for more than half (52.18%) of the total number of species, and individually were the only families in the sample which accounted for greater than 5% of the total number of trees. In decreasing order of abundance these families were: Rubiaceae (15.05%), Lauraceae (9.42%), Myrtaceae (8.10%), Myrsinaceae (6.7%), Apocynaceae (6.58%), and Monimiaceae (6.33%).

Talatakely: Species, genus, and family richness are listed overall in Table 2.2 and by plot in Table 2.4. Tagged trees and lianas in the three plots in Talatakely belonged to a minimum of 45 different families; 24 individuals were unidentified at the family level. 17 families in Talatakely were rare; 8 of these families were represented by a single individual. As in the total sample, the 6 most abundant families at this site accounted for more than half (52.72%) of all trees in the plots and all other families accounted for approximately 5% or less at this site. In decreasing order of abundance the best represented families were: Rubiaceae (12.85%), Lauraceae (10.69%), Monimiaceae (7.81%), Myrtaceae (7.81%), Apocynaceae (7.19%), and Cyatheaceae (6.37%, composed of a species poorly represented in Vatoharanana). A K-means cluster analysis was applied to the sample of families according to relative abundance scores. Cluster 1 consisted of the top 8 families and cluster 2 consisted of the remaining families. The top 5 most abundant families, genera, and species are listed in Table 2.5. 8 families were

unique to Talatakely (Table 2.7a). All unique families were represented by 9 or fewer individuals.

Total basal area/ha for all stems $\geq$ 10 cm DBH in Talatakely was 33.21 m^2 (n=873) (Table 2.3). *Weinmannia bojeriana* (Cunoniaceae, 'Maka') was the relatively most dominant species present at this site (Table 2.6a). Lauraceae, one of the most abundant families in Talatakely, accounted for the largest proportion of standing biomass on both the generic and familial levels (Table 2.6bc).

Vatoharanana: Species, genus, and family richness are listed overall in Table 2.2 and by plot in Table 2.4. Tagged trees and lianas in the three plots in Vatoharanana belonged to a minimum of 41 different families; 7 individuals were unidentified at the family level. No significant differences were found between sites in species richness (X^2(1,n=6)=0.049, p=0.83 ns), genus richness (X^2(1,n=6)=0.048, p= 0.83 ns), or family richness (X^2(1,n=6)=0.196, p=0.66 ns). As in the total sample and the Talatakely sample, the 6 most abundant families at this site accounted for more than half (54.61%) of all trees in the plots. All other families individually accounted for less than 5% of all trees in the site. In decreasing order the most abundant families were: Rubiaceae (18.59%), Myrsinaceae (9.21%), Myrtaceae (8.55%), Lauraceae (7.40%), Apocynaceae (5.59%), and Oleaceae (5.26%). A K-means cluster analysis was applied to the sample of families according to relative abundance scores. Cluster 1 consisted solely of the most abundant family, Rubiaceae, while cluster 2 consisted of all remaining families. Vatoharanana was overwhelmingly dominated in relative abundance by Rubiaceae in each plot as well as the site as a whole (Tables 2.4 and 2.5). The greater relative abundance of Lauraceae in Talatakely compared with Vatoharanana reduced the relative abundance of the top family, Rubiaceae, in that site (Tables 2.4 and 2.5). The top 5 most abundant families,

genera, and species are listed in Table 2.5. 5 families were unique to Vatoharanana (Table 2.7b). All unique families were represented by 3 or fewer individuals.

As indicated above, total basal area/ha for all stems $\geq$ 10 cm DBH at this site (71.31 m^2 (n=539)) was more than twice that in Talatakely (Table 2.3), indicating less forest biomass and production in Talatakely (independent samples t-test: t(1411)=6.069, $p<.001$). *Chrysophyllum boivinianium* (Sapotaceae, 'Rahiaka') had the highest relative dominance of all species present at this site (Table 2.6a) and Lauraceae, one of the most abundant families in Vatoharanana, also accounted for the largest proportion of standing biomass on both the generic and familial levels (Table 2.6bc), as was the case in Talatakely. A comparison of the proportion of relative dominance to relative abundance highlights the lower density of large diameter stems, or less species occupying positions of dominance (Balko and Underwood, 2005) in Talatakely (27.03% of families) relative to Vatoharanana (46.15% of families) (Figure 2.3, Table 2.7). It is notable however that Rubiaceae in Talatakely had a score more than double the most dominant family in Vatoharanana.

Table 2.2. Forest characteristics for study sites in Ranomafana National Park. Data were collected September 2003, except where indicated. Asterisks indicate significant site differences. Highest values are bolded for each parameter.

Characteristic	**Talatakely (heavily logged)**	**Vatoharanana (selectively logged)**
Mean Diameter at Breast Height (cm) ± SD (N)***	7.10 ± 6.62 (873)	**11.25 ± 12.17 (539)**
Mean Tree Height (m) ± SD (N)**	8.57 ± 5.01 (884)	**9.63 ± 6.55 (542)**
Mean Crown Diameter (m) ± SD (N)	**2.59 ± 2.15 (886)**	2.47 ± 2.06 (542)
Mean Crown Depth (m) ± SD (N)**	3.09 ± 2.54 (886)	**3.19 ± 3.29 (542)**
Mean Crown Volume (m^3) ± SE[1]	198.52 ± 37.63	**238.73 ± 16.68**
Mean Basal Area (m^2) (N)***	0.007 (873)	**0.02 (539)**
Total Basal Area/ha (m^2) (N), CV	33.21 (873), 0.329	**71.31 (539), 0.326**
Species Richness (N)	113 (973)	**123 (630)**
Evenness (N)	0.85 (973)	**0.88 (630)**
Shannon & Wiener Diversity Index (N)		
Site Species Diversity	4.02 (973)	**4.21 (630)**
Site Structural Diversity	4.75 (226)	**4.84 (264)**
Simpson Diversity Index (N)[2]		
Site Species Diversity	0.970 (973)	**0.980 (630)**
Site Structural Diversity	0.990 (226)	**0.991 (264)**

[1]Crown Volumes from Balko, 1998. Shannon-Weiner Diversity Index (H)=Σ (pi) (ln pi), where pi=relative density of the ith species, is a measure of species diversity.
[2]Simpson Diversity Index: A lower score indicates more diversity.

Table 2.3. Total basal area per hectare for each plot in Talatakely and Vatoharanana. Large trees are all trees in plots which were > 10cm DBH; small trees are all trees in plots which were <10cm DBH. Plot basal area/ha is the sum total basal area/ha for each plot in each site. Total basal area/ha is included for each site. Asterisks indicate significant differences between total basal area/ha among sites.

Site	Plot/size (m^2)	Basal Area/ha Large Trees (m^2) (N)	Basal Area/ha Small Trees (m^2) (N)	Plot Basal Area/ha (m^2) (N)
Vato	1/1000	80.04 (140)	6.23 (224)	86.27 (364)
Vato	2/250	74.58 (62)	5.75 (62)	80.33 (83)
Vato	3/250	33.10 (27)	6.10 (68)	39.20 (92)
		Vatoharanana Basal Area/ha Large Trees (m^2) (N)		**71.31 (539)*** **

Site	Plot/size (m^2)	Basal Area/ha Large Trees (m^2) (N)	Basal Area/ha Small Trees (m^2) (N)	Plot Basal Area/ha (m^2) (N)
Tala	1/250	12.09 (16)	7.67 (110)	19.75 (126)
Tala	2/250	0.84 (153)	11.05 (2)	11.88 (155)
Tala	3/1000	46.58 (461)	10.04 (131)	56.62 (592)
		Talatakely Basal Area/ha Large Trees (m^2) (N)		**33.21 (873)*** **

Table 2.4. Species richness and forest community composition for each plot in Talatakely and Vatoharanana.

Site/Plot	Family	Genus	Species	Top Family	Percent	Second Family	Percent
Tala 1	28	37	54	Monimiaceae	14.59%	Rubiaceae	14.05%
Tala 2	21	25	30	Myrtaceae	26.67%	Rubiaceae	13.94%
Tala 3	42	61	93	Lauraceae	13.48%	Rubiaceae	11.88%
Vato 1	39	60	96	Rubiaceae	18.18%	Myrsinaceae	10.23%
Vato 2	28	38	48	Rubiaceae	16.67%	Lauraceae	10.00%
Vato 3	29	36	48	Rubiaceae	17.00%	Monimaceae, Myrtaceae	11.00%

Table 2.5. Relative abundance of vegetation in Talatakely and Vatoharanana. The top 5 (A) species, (B) genera, and (C) families in each site.

(A) Top 5 Species

	Family	Species	Vernacular	Relative Abundance
Tala	Rubiaceae	*Psychotria* sp. "fohaninasity"	Fohaninasity	7.91
	Cyatheaceae	*Cyathea* sp. "faho"	Faho	6.37
	Apocynaceae	*Mascarenhasia arborescens* A. DC.	Herodrano	6.27
	Monimiaceae	*Tambourissa* sp. "kibilany"	Kibilany	4.63
	Myrsinaceae	*Oncostemum acuminatum*	Kalafambakaka	4.52
Vato	Rubiaceae	*Psychotria* sp. "fohaninasity"	Fohaninasity	7.24
	Myrsinaceae	*Oncostemum* sp. "kalafambakaka pf"	Kalafambakaka pf	7.07
	Rubiaceae	*Psychotria* sp. "ranjopody"	Ranjopody	5.26
	Myrtaceae	*Syzygium* sp. "rotra fotsy"	Rotra fotsy	4.44
	Myrtaceae	*Syzygium* sp. "rotra mena"	Rotra mena	3.13

(B) Top 5 Genera

	Family	Genus	Relative Abundance
Tala	Rubiaceae	*Psychotria*	8.22
	Monimiaceae	*Tambourissa*	7.81
	Cyatheaceae	*Cyathea*	6.37
	Apocynaceae	*Mascarenhasia*	6.27
	Lauraceae	*Cryptocarya*	6.27
Vato	Rubiaceae	*Psychotria*	12.50
	Myrsinaceae	*Oncostemum*	9.21
	Myrtaceae	*Syzygium*	8.55
	Lauraceae	*Cryptocarya*	5.92
	Oleaceae	*Noronhia*	5.26

(C) Top 5 Families

	Family	Relative Abundance
Tala	Rubiaceae	12.85
	Lauraceae	10.69
	Myrtaceae	7.81
	Monimiaceae	7.81
	Apocynaceae	7.19
Vato	Rubiaceae	18.59
	Myrsinaceae	9.21
	Myrtaceae	8.55
	Lauraceae	7.40
	Apocynaceae	5.59

Table 2.6. Relative dominance of vegetation in Talatakely and Vatoharanana. The top 5 (A) species, (B) genera, and (C) families in each site.

(A) Top 5 Species

	Family	Species	Vernacular	Relative Dominance
Tala	Cunoniaceae	*Weinmannia bojeriana* Tul.	Maka	10.02
	Clusiaceae	*Calophyllum* sp. "vitanona"	Vitanona	8.37
	Apocynaceae	*Mascarenhasia arborescens* A. DC.	Herodrano	7.22
	Lauraceae	*Cryptocarya* sp. "tavolo manitra"	Tavolo manitra	4.88
	Lauraceae	*Cryptocarya* cf. "flavescens"	Tavolo maintso	4.57
Vato	Sapotaceae	*Chrysophyllum boivinianium* (Pierre) Baehni	Rahiaka	4.70
	Myrsinaceae	*Oncostemum* sp. "kalafambakaka pf"	Kalafambakaka pf	4.19
	Myrtaceae	*Syzygium* sp. "rotra fotsy"	Rotra fotsy	4.01
	Elaeocarpaceae	*Sloanea rhodantha* var. *rhodantha* (Baker) Capuron	Vanana	3.91
	Monimiaceae	*Tambourissa thouvenotii*	Ambora	3.71

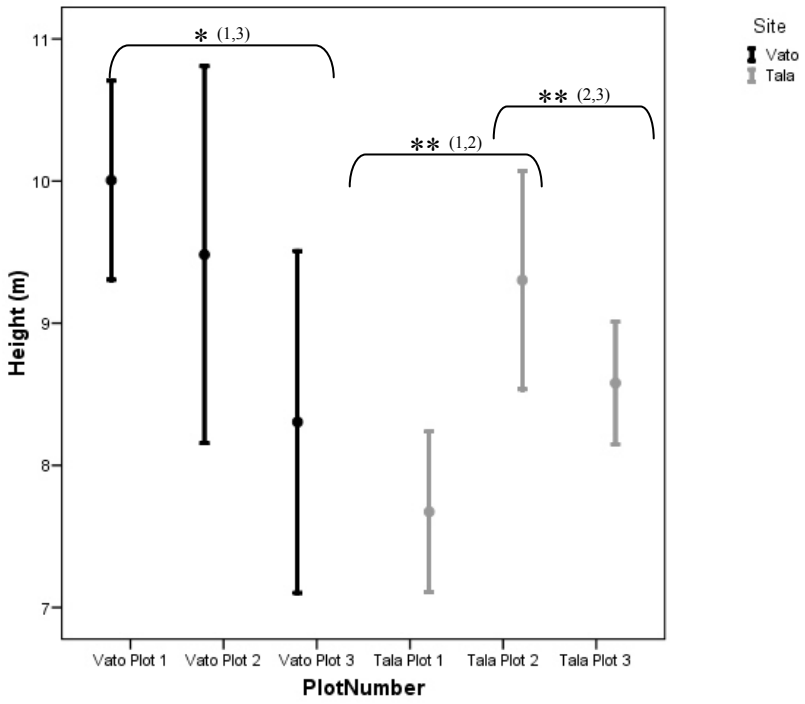
(B) Top 5 Genera

	Family	Genus	Relative Dominance
Tala	Lauraceae	*Cryptocarya*	14.17
	Cunoniaceae	*Weinmannia*	10.26
	Clusiaceae	*Calophyllum*	8.37
	Apocynaceae	*Mascarenhasia*	7.22
	Monimiaceae	*Tambourissa*	5.74
Vato	Lauraceae	*Cryptocarya*	9.74
	Myrtaceae	*Syzygium*	8.19
	Monimiaceae	*Tambourissa*	5.83
	Myrsinaceae	*Oncostemum*	5.38
	Rubiaceae	*Psychotria*	5.13

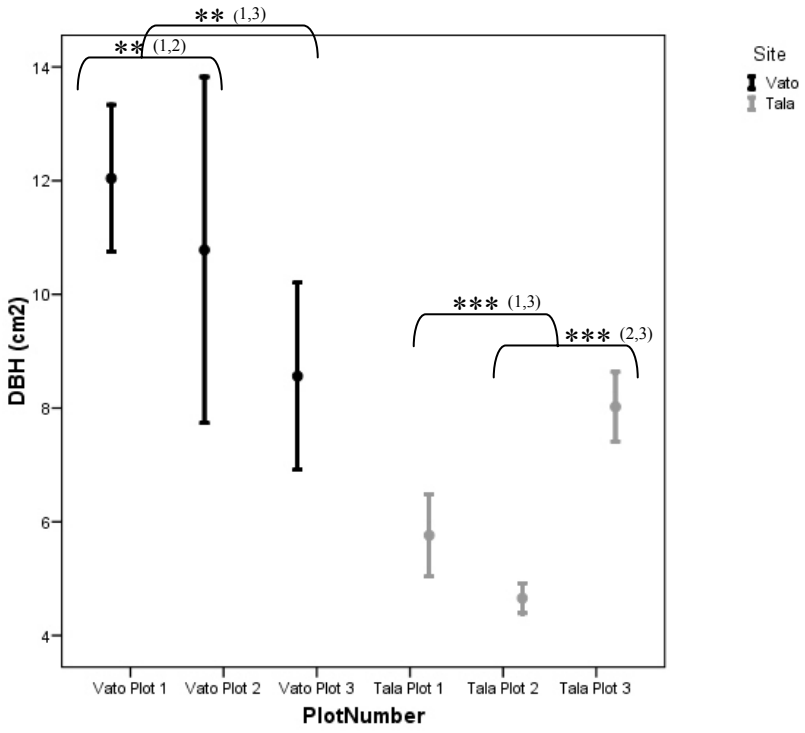
(C) Top 5 Families

	Family	Relative Dominance
Tala	Lauraceae	20.45
	Clusiaceae/Guttiferaceae	10.76
	Cunoniaceae	10.26
	Apocynaceae	7.22
	Myrtaceae	5.91
Vato	Lauraceae	14.05
	Rubiaceae	9.75
	Myrtaceae	8.19
	Leguminosae	6.09
	Monimiaceae	5.83

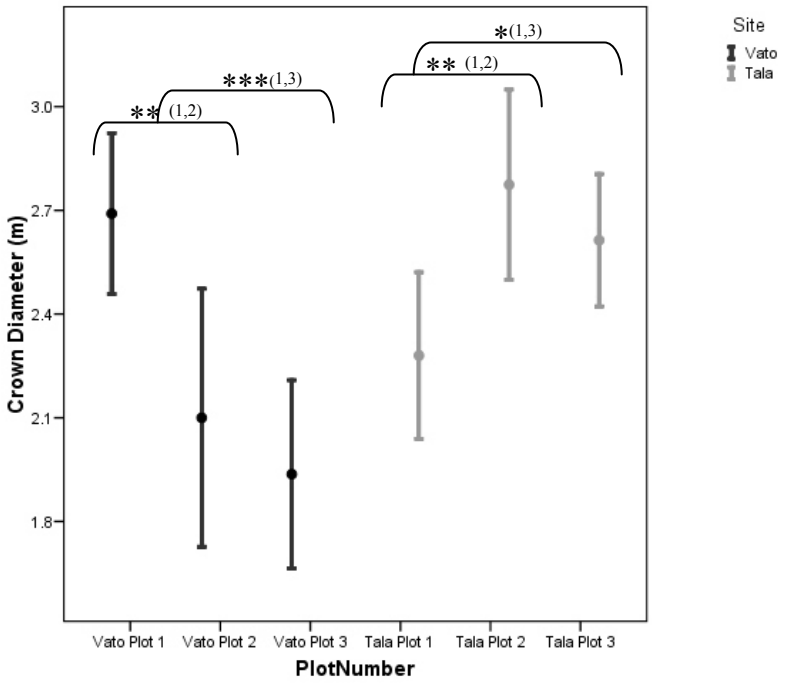
(A)


* (1,3)
** (2,3)
** (1,2)
Site
Vato
Tala
Height (m)
11
10
9
8
7
Vato Plot 1
Vato Plot 2
Vato Plot 3
Tala Plot 1
Tala Plot 2
Tala Plot 3
PlotNumber

(B)


** (1,3)
** (1,2)
*** (1,3)
*** (2,3)
Site
Vato
Tala
DBH (cm2)
14
12
10
8
6
4
Vato Plot 1
Vato Plot 2
Vato Plot 3
Tala Plot 1
Tala Plot 2
Tala Plot 3
PlotNumber

(C)



(D)

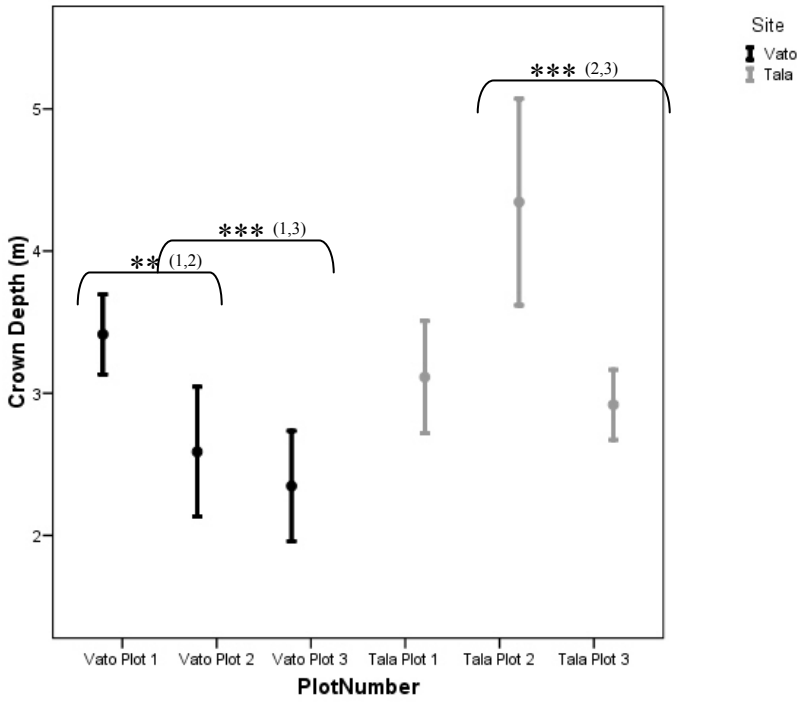


Figure 2.2. Structural measures for each botanical plot in each site. 95% confidence intervals surround the mean. (A) Height; (B) DBH; (C) Crown diameter; and (D) Crown depth. Numbers in parentheses indicate significantly different pairs within each site.

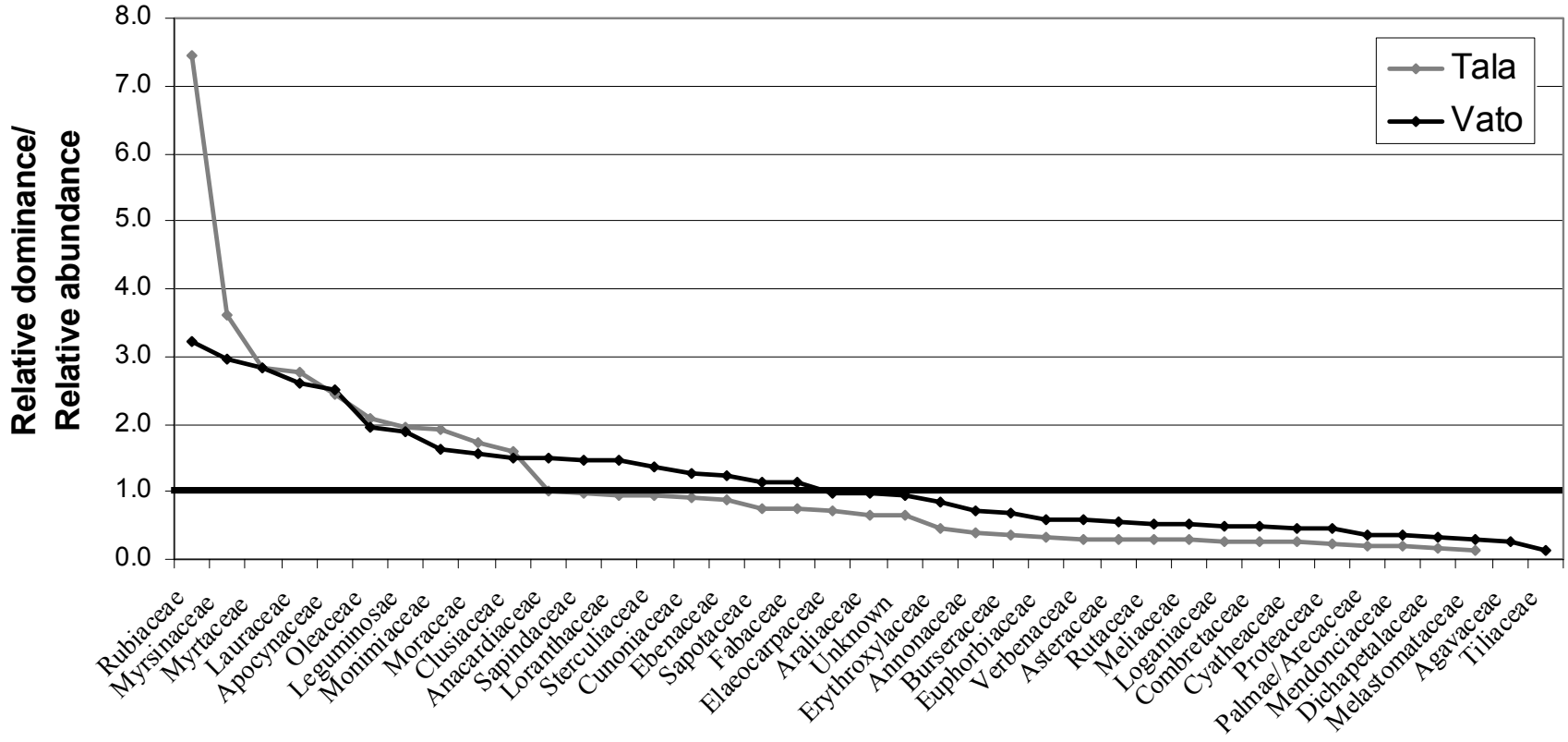


Figure 2.3. Relationship between relative dominance and abundance in Talatakely and Vatoharanana (RD/RA). RD > RA (a value >1) indicates lower density of large diameter stems; a value <1 indicates a higher density of small diameter stems.

Table 2.7. Relative abundance and relative dominance in (A) Talatakely and (B) Vatoharanana. Bolded text indicates families which were located in only one site. Italics indicate families exploited in only one site. Note that not all exploited families are listed, as they were not located in botanical plots[1].

(A) Tala

Family	Relative Abundance	Relative Dominance
Rubiaceae	12.85	4.47
Lauraceae	10.69	20.45
Myrtaceae	7.81	5.91
Monimiaceae	7.81	5.74
Apocynaceae	7.19	7.22
Cyatheaceae	6.37	2.89
Clusiaceae/Guttiferaceae	5.14	10.76
Myrsinaceae	5.14	1.51
Moraceae	4.11	3.81
Cunoniaceae	3.70	10.26
Araliaceae	2.98	1.98
Unknown	2.47	0.66
Euphorbiaceae	2.36	4.60
Anacardiaceae	1.85	1.80
Leguminosae	1.64	2.60
Tiliaceae	1.44	3.52
Sapindaceae	1.44	1.36
Rutaceae	1.44	0.38
Sterculiaceae	1.34	1.27
Oleaceae	1.03	0.24
Smilaceae	0.92	N/A (liana)
Melastomataceae	0.82	0.73
Fabaceae	0.82	0.31
Loganiaceae	0.82	0.24
Aquifoliaceae	0.72	2.60
Ebenaceae	0.72	0.20
Mendonciaceae	0.62	N/A (liana)
Piperaceae	0.62	N/A (liana)
Flacourtiaceae	0.62	0.19
Meliaceae	0.62	0.11
Elaeocarpaceae	0.51	1.45
Vitaceae	0.41	N/A (liana)
Annonaceae	0.41	0.70
Pittosporaceae	0.41	0.12
Dichapetalaceae	0.31	N/A (liana)
Pandanaceae	0.31	0.22
Agavaceae	0.31	0.05
Erythroxylaceae	0.31	0.04
Burseraceae	0.21	1.53
Loranthaceae	0.10	N/A (liana)
Menispermaceae?	0.10	N/A (liana)
Rhamnaceae	0.10	N/A (liana)
Schizeaceae	0.10	N/A (liana)
Verbenaceae	0.10	0.07
Sapotaceae	0.10	0.03
Asteraceae	0.10	0.02

(B) Vatoharanana

Family	Relative Abundance	Relative Dominance
Rubiaceae	18.59	9.75
Myrsinaceae	9.21	5.38
Myrtaceae	8.55	8.19
Lauraceae	7.40	14.05
Apocynaceae	5.59	4.71
Oleaceae	5.34	2.58
Leguminosae	4.77	6.09
Monimiaceae	3.95	5.83
Moraceae	3.13	3.82
Clusiaceae	3.13	3.02
Anacardiaceae	2.80	4.18
Sapindaceae	3.12	3.11
Loranthaceae	2.30	0.82
Sterculiaceae	1.97	1.91
Cunoniaceae	1.81	4.50
Ebenaceae	1.81	1.08
Sapotaceae	1.64	5.29
Fabaceae	1.48	N/A (liana)
Elaeocarpaceae	1.32	3.91
Araliaceae	1.32	0.40
Unknown	1.15	0.80
Erythroxylaceae	0.99	1.92
Annonaceae	0.82	1.33
Burseraceae	0.82	1.28
Euphorbiaceae	1.23	0.52
Verbenaceae	0.66	0.91
Asteraceae	0.66	0.31
Rutaceae	0.66	0.30
Meliaceae	0.66	0.25
Loganiaceae	0.49	1.28
Combretaceae	0.49	0.72
Cyatheaceae	0.49	0.23
Proteaceae	0.33	0.50
Palmae/Arecaceae	0.33	0.17
Mendonciaceae	0.33	N/A (liana)
Dichapetalaceae	0.33	N/A (liana)
Melastomataceae	0.16	0.47
Agavaceae	0.16	0.19
Tiliaceae	0.16	0.12
Flacourtiaceae	0.16	0.05
***Icacinaceae*/Mimosaceae/Cannellaceae**	0.16	0.04
Connaraceae	0.16	N/A (liana)
Aquifoliaceae	0.16	N/A (liana)

[1] Families exploited only in Talatakely, but not represented in botanical plots: Compositae, Passifloraceae. Families exploited only in Vatoharanana, but not represented in botanical plots: Ochnaceae, Solanaceae, Torricelliaceae.

Forest community diversity: diversity indices

Indices of diversity (Shannon and Wiener Diversity Index and Simpson's Diversity Index) estimated that Vatoharanana had greater species and structural diversity (Table 2.2) and species evenness. Indices were calculated for each plot to test for significant differences across sites, and no differences were found (Table 2.8). This is most likely a relic of small sample size combined with differences in microhabitat within sites. Since only trees between 10 and 30 cm DBH were used for analyses of structural diversity and plot sizes varied, variation between plot sample sizes was great (Table 2.8).

Table 2.8. Species and structural diversity indices for botanical plots in Vatoharanana and Talatakely in Ranomafana National Park. H is the test statistic for the Shannon and Wiener Index. D is the test statistic for Simpson's Diversity Index.

Site/Plot	H Species (N)	H Structure (N)	D Species (N)	D Structure (N)
Talatakely 1	3.56 (54)	2.69 (16)	0.96 (54)	0.93 (16)
Talatakely 2	2.80 (30)	0.69 (2)	0.90 (30)	0.50 (2)
Talatakely 3	3.84 (93)	4.60 (114)	0.96 (93)	0.99 (114)
Vatoharanana 1	3.68 (98)	4.57 (112)	0.97 (98)	0.99 (112)
Vatoharanana 2	4.03 (48)	2.42 (13)	0.97 (48)	0.90 (13)
Vatoharanana 3	3.52 (48)	2.97 (22)	0.96 (48)	0.94 (22)

Climate Seasons

Temperature

Daily temperatures in Talatakely ranged from 9˚ C to 32˚ C and mean monthly minimum and maximum temperatures ranged from 12.21˚ C (August 2004) to 25.8˚ C (February 2005), with mean values of 16.32 $\pm$ 2.22 and 22.41 $\pm$ 2.63˚ C respectively. Mean monthly temperatures, calculated as the average of minimum and maximum temperatures each month, were lowest in August 2004 and highest in January 2005 (Figure 2.4a).

Daily temperatures in Vatoharanana ranged from 7˚ C to 35˚ C and mean monthly minimum and maximum temperatures ranged from 8.22˚ C (March 2005) to 27.73˚ C (November 2003), with means of 9.57 ± 1.10 and 24.39 ± 1.71˚ C respectively. Mean monthly temperatures were lowest in July 2004 and were highest in November 2003 (Figure 2.4b).

In both sites combined, mean monthly temperatures ranged from 15.14˚ C (June 2004) to 19.81˚ C (February 2004) (Figure 2.4c). The cold season was approximately April through October and the warm season was approximately November through February/March during the course of this study.

Rainfall

There was a slight bimodal trend in rainfall (Figure 2.4). Large ranges for rainfall totals exemplify the variation present in this rain forest. Daily rainfall in Talatakely ranged from 0 mm to 126 mm and monthly rainfall totals ranged from 10 mm (October 2003) to 599 mm (January 2004) (Figure 2.4a). Daily rainfall in Vatoharanana ranged from 0 mm to 202 mm and monthly rainfall totals ranged from 2 mm (October 2003) to 998 mm (February 2004) (Figure 2.4b). Site differences are possible, yet such an extreme disparity between the sites in the upper range of rainfall may be due to the frequency with which the rain gauge was emptied during high rainfall days, and therefore the higher value is more likely to be accurate. The average of total monthly rainfall in both sites combined ranged from 6 mm (October 2003) to 722 mm (February 2005) (Figure 2.4c). The average total monthly rainfall for the two complete wet seasons (December through March, >300 mm) was 2050 mm in 2003/2004 and 2263 mm in 2004/2005. The average total monthly rainfall for the complete dry season (April through November 2004, < 300 mm) was 1644 mm (Figure 2.4c).

Temperature and Rainfall

Because rainfall was unevenly distributed, nonparametric tests were used to investigate the relationship between rainfall and temperature. Rainfall and average monthly temperature were significantly correlated (Spearman's rho 0.60, n=18, $p<.01$). Rainfall and minimum, but not maximum, temperature were significantly correlated, though the significant correlation is quite small (Spearman's rho minimum temperature: 0.064, n=1088, $p<.05$; Spearman's rho maximum temperature: -0.030, n=1088, ns). When temperatures were low rainfall was low; when temperatures were high there was more variability in rainfall (Figure 2.5). This may be a result of the inability to consistently empty rain gauges more than once per day while in Talatakely, which would present variability in rainfall measures during periods of high rainfall. More likely, or in addition, the drier season was largely cool with slightly rising temperatures, while an entirely dry wet season did not occur; in contrast both cool and warm wet seasons occurred.

Cyclone Elita hit Ranomafana in early February 2004 and was characterized by very strong winds and heavy rain. While the Indian Ocean experienced a devastating tsunami event in December 2004 the effects of which mildly impacted coastal towns in Madagascar, no cyclones occurred in Ranomafana in the 2004-2005 cyclone season (typically December through March).

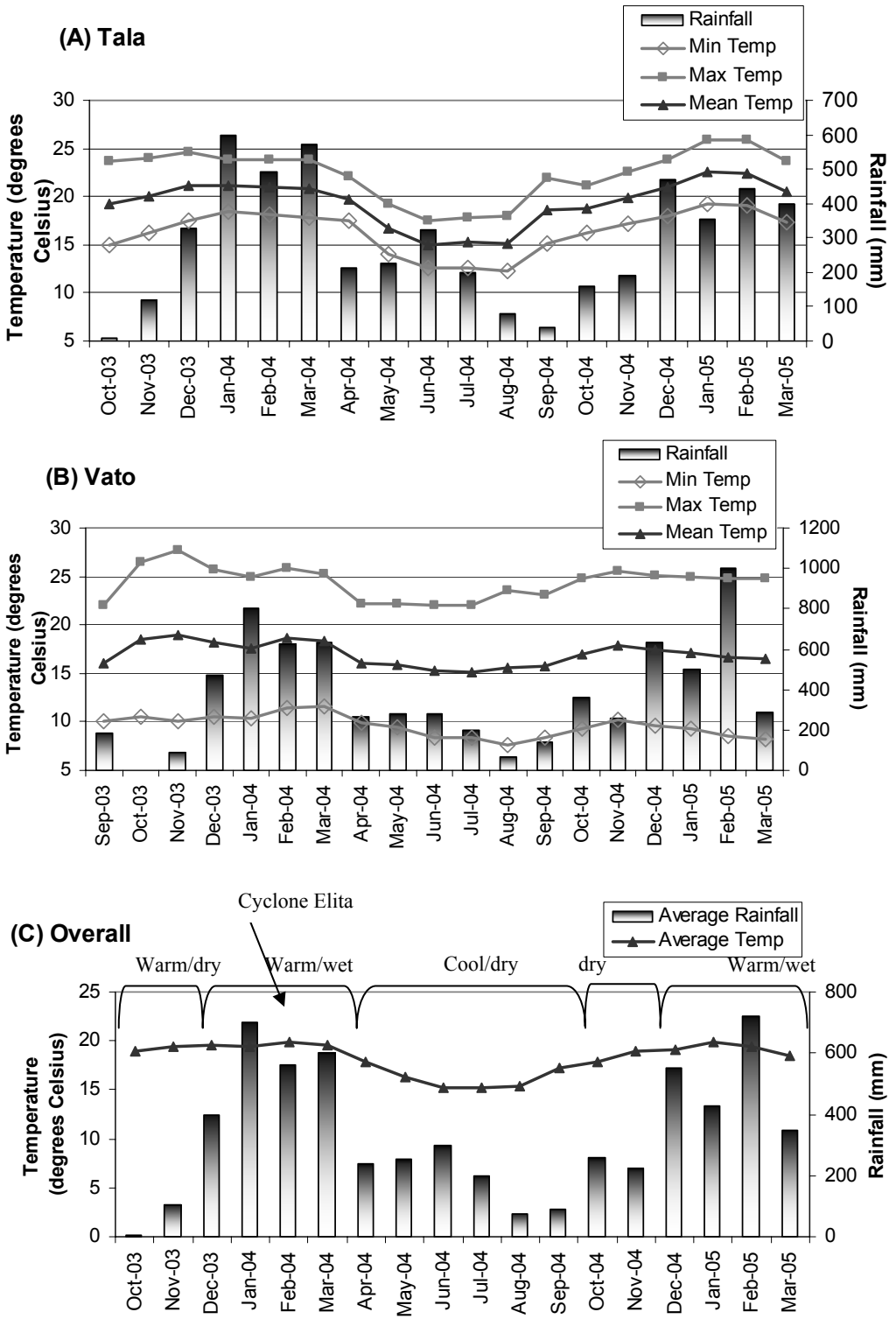


Figure 2.4. Monthly minimum, maximum, and mean temperatures and total rainfall in (A) Tala, (B) Vato, and (C) averaged overall.

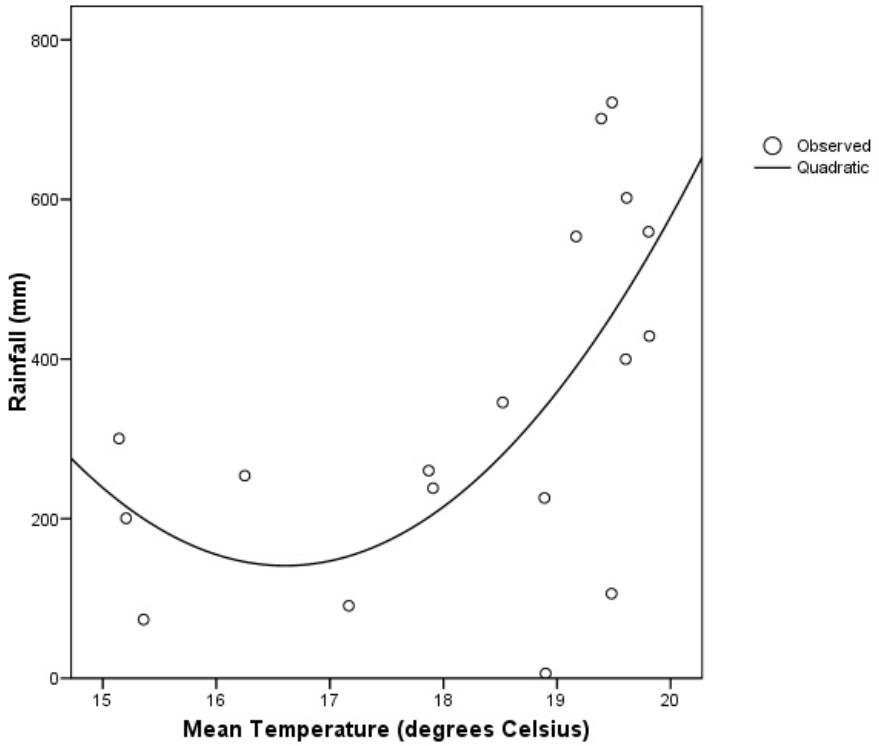


Figure 2.5. Regression of mean temperature and rainfall.

Phenology and Food Availability Seasons

Food abundance and scarcity seasons did not coincide with previous studies (see Overdorff, 1991 and Overdorff & Tecot, 2006), and differences between sites were apparent. The availability of leaves, fruits, and inflorescences (flower buds, petals, and blooms) was seasonal, as was also indicated by coefficients of dispersion (see above) (Figure 2.6). The results for leaf flushing in September, the first month of the study, appear abnormally low and drove the low overall percentage of available food in that month. Consequently, September leaf flushing data were not included in the remaining analyses.

Fruit

Measures of fruit availability seasons in this study were drastically different depending upon how resources were combined for analysis due to the much higher abundance of unripe fruit during ripe fruit scarcity or absence (Figures 2.7a and 2.8a), particularly in Talatakely (Tecot, Chapter 3). For instance, when unripe fruit is viewed alone or in combination with ripe fruit in Talatakely, March 2004 is a period of abundance. However, *no ripe fruit* was present at this site in March; according to the availability of ripe fruit March is a period of scarcity (Figure 2.7a). Both ripe and unripe fruit are important components of the diet, yet their nutritional values may differ and affect time budgets differently. To determine food availability seasons, data were analyzed in two ways: by total fruit availability and by ripe fruit availability (which will allow investigation of the impact of unripe fruit as well). Resource availability seasons for each site are summarized in Table 2.9. Fruit availability seasons which were determined using Dataset 2, consisting only of species which *Eulemur rubriventer* consumed, were consistent with these patterns (Figures 2.7c and 2.8c).

Total fruit availability showed a similar pattern throughout the study at each site, and was loosely synchronized across sites (Figures 2.7a, 2.8a, and 2.9a) with a more normal distribution and clearer delineations between scarce and abundant seasons in Vatoharanana. Fruit abundance in Talatakely was more unpredictable, and lower than in Vatoharanana throughout the year (note scale differences in figures). The same pattern with less noise emerged from Dataset 2. In Talatakely the impact of January's fruit abundance and the disparity between July and August were diminished, and March emerged as a major period of food abundance (Figure 2.10).

It bears noting that the *only* resource exploited in Talatakely in March 2004 was unripe fruit from *Psidium cattleianum,* Chinese guava (Figure 2.11), despite the presence

of fruit on six other species which were exploited for fruit during other months (Figure 2.12). This species is a non-native, invasive species present only in Talatakely and appears to be a preferred resource whether ripe or unripe.

Leaves

Leaf flushing was unsynchronized within and between sites and more new leaves were available in Vatoharanana than in Talatakely throughout the study (Figure 2.9b). Talatakely experienced a sink in new leaf availability in July. No true scarcity period occurred in Vatoharanana, though flushing in August-September was slightly lower. New leaf availability peaked in Talatakely in November 2004 (Figure 2.9b) when 785 trees in botanical plots were flushing, and only four species accounted for approximately 25% (Table 2.10a). New leaf availability in Vatoharanana peaked in February of each year (Figure 2.9b), when 526 trees in botanical plots were flushing, and only five species accounted for approximately 25% (Table 2.10b). Fohaninasity *(Psychotria sp.)* had the largest percentage of new leaves in both sites, and Kalafambakaka *(Oncostemon sp.)* was in the top 5 in both sites (Table 2.10). Kalafambakaka is the only one of these species from which red-bellied lemurs exploited new leaves throughout the study, but all of these species were exploited for different plant parts. An almost identical result was found using only Dataset 2 with the exception that new leaf availability in Talatakely was elevated above that in Vatoharanana between December-January 2003 and October-November 2004 (Figure 2.10b).

Flowers

Flowering was highly synchronized at each site and loosely synchronized across sites (Figure 2.9c). In Talatakely flowering was highest in June and July, when fruit availability was declining and low (Figure 2.9a) and new leaves were scarce (Figure

2.9b). 36 trees from 7 species in botanical plots flowered at this time in Talatakely (Table 2.11a). In Vatoharanana flowering was highest in January of each year. Peak flowering occurred in December 2003/January 2004 when fruit availability was declining and low (Figure 2.9a) and new leaves were relatively scarce (Figure 2.9b). 77 trees from 15 species in botanical plots flowered at this time in Vatoharanana (Table 2.11b). Throughout the study, only two of these species were exploited in Vatoharanana and one was exploited in Talatakely (Table 2.11). However, flowering in exploited species (Dataset 2) was also highly synchronous within sites and peaks were similarly timed (Figures 2.9c and 2.10C).

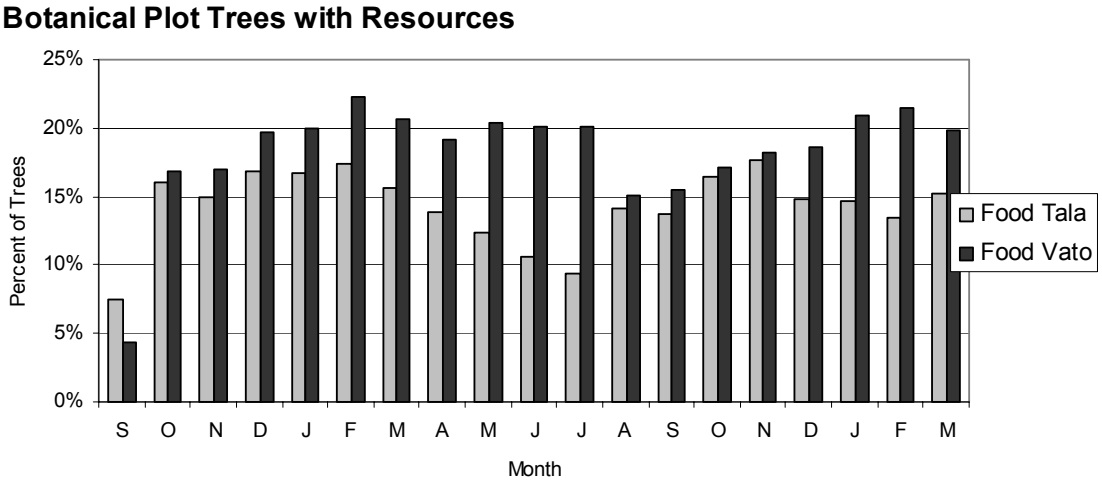


Figure 2.6. Availability of leaves, fruits, and inflorescences from September 2003 through December 2005 by site.

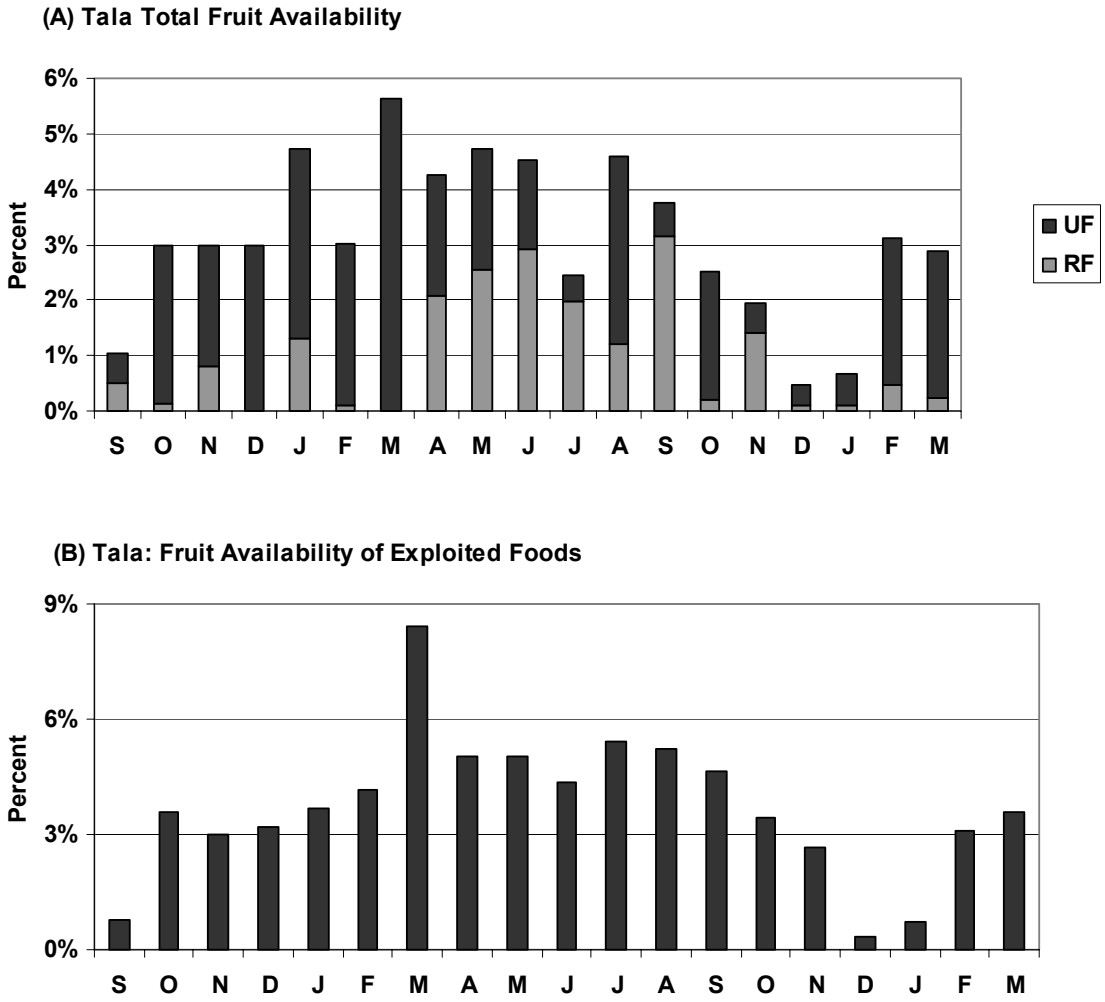


Figure 2.7. Fruit availability in Talatakely between September 2003 and March 2005. (A) Percent of trees in Talatakely botanical plots with scores of 1-5 for ripe (RF) or unripe (UF) fruit each month. (B) Percent of trees in Talatakely botanical plots belonging to species exploited by *Eulemur rubriventer* for fruit during the study with scores of 1-5 for RF or UF.

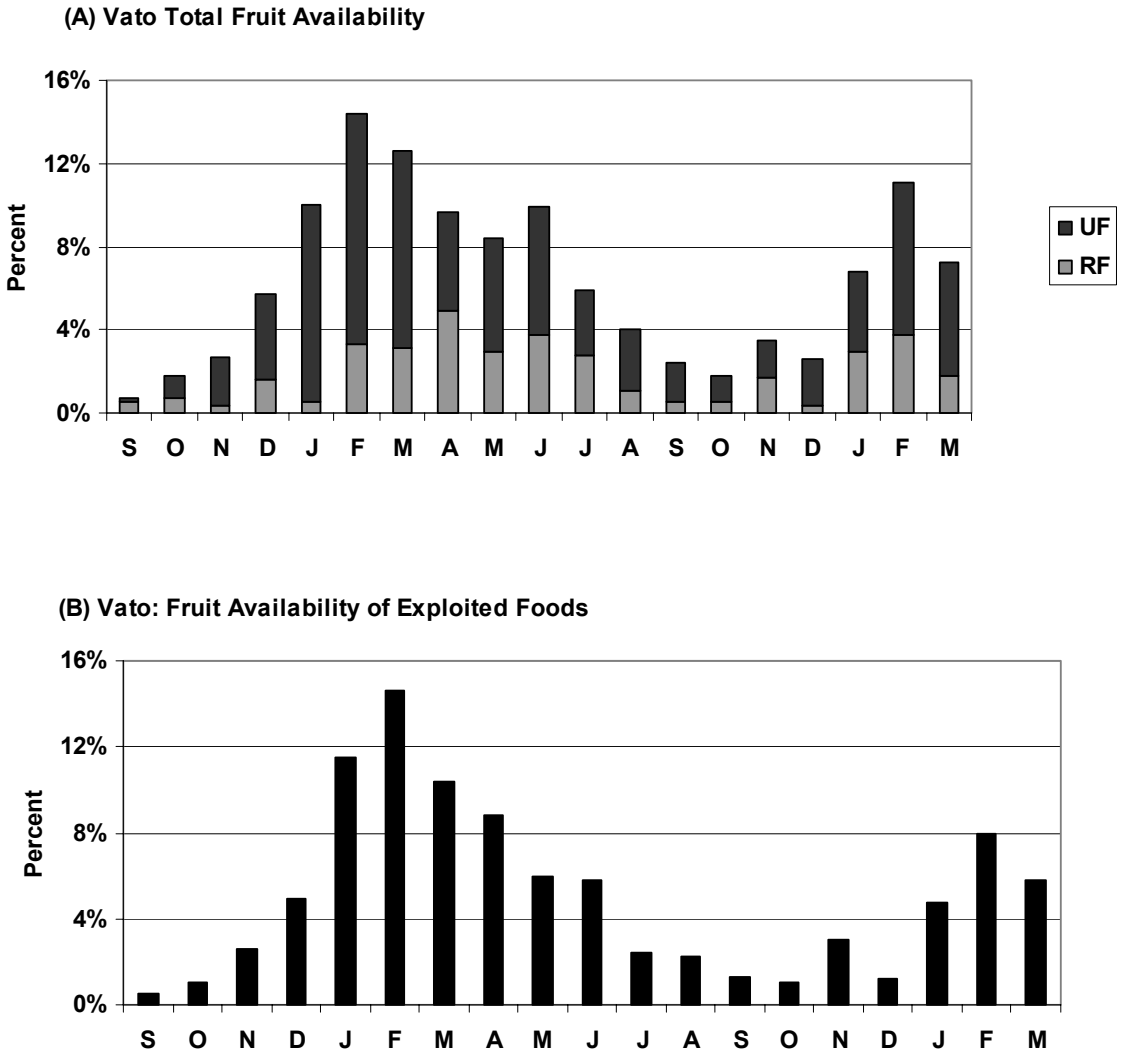
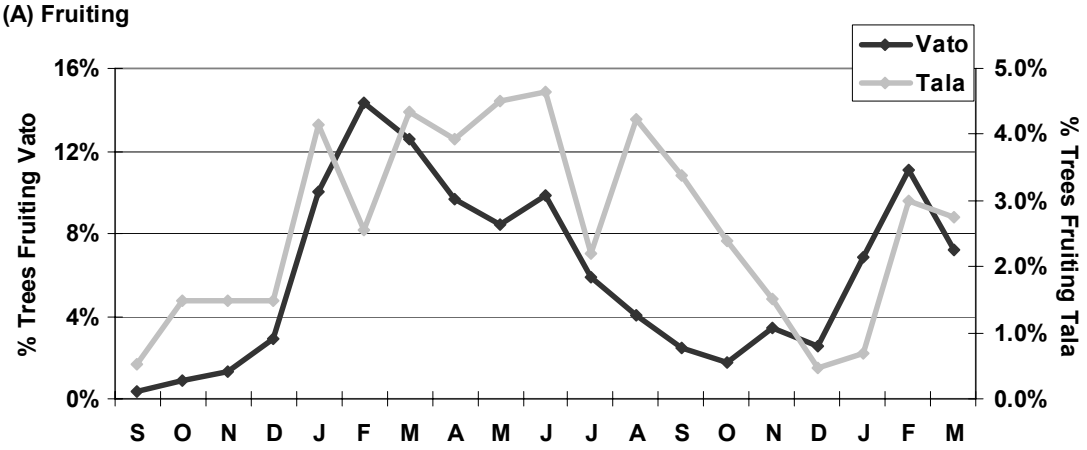


Figure 2.8. Fruit availability in Vatoharanana between September 2003 and March 2005. (A) Percent of trees in Vatoharanana botanical plots with scores of 1-5 for ripe (RF) or unripe (UF) fruit each month. (B) Percent of trees in Talatakely botanical plots belonging to species exploited by *Eulemur rubriventer* during the study with scores of 1-5 for RF or UF.

Table 2.9. Food abundance and scarcity seasons in Talatakely and Vatoharanana in Ranomafana National Park, Madagascar between January, 2004 and March, 2005. Abundance and scarcity seasons were determined by the availability scores of ripe fruit and the combination of ripe and unripe fruit on botanical plot trees, and were determined only for those months in which behavioral data were collected (January 2004 – March 2005).

Site	Ripe Fruit Abundance Months	Ripe Fruit Scarcity Months	Total Fruit Abundance Months	Total Fruit Scarcity Months
Tala	Jan, Apr-Jul, Sep, Nov 2004	Feb-Mar, Aug, Oct, Dec 2004 Jan-Mar 2005	Jan-Jun, Aug-Sep 2004 Feb-Mar 2005	July, Sep-Dec 2004 Jan 2005
Vato	Feb-Jul 2004, Jan-Feb[1] 2005	Jan, Aug-Dec 2004 Mar 2005	Jan-Jul 2004 Jan-Mar 2005	Aug-Dec 2004

[1]Study ended at the close of March, 2005



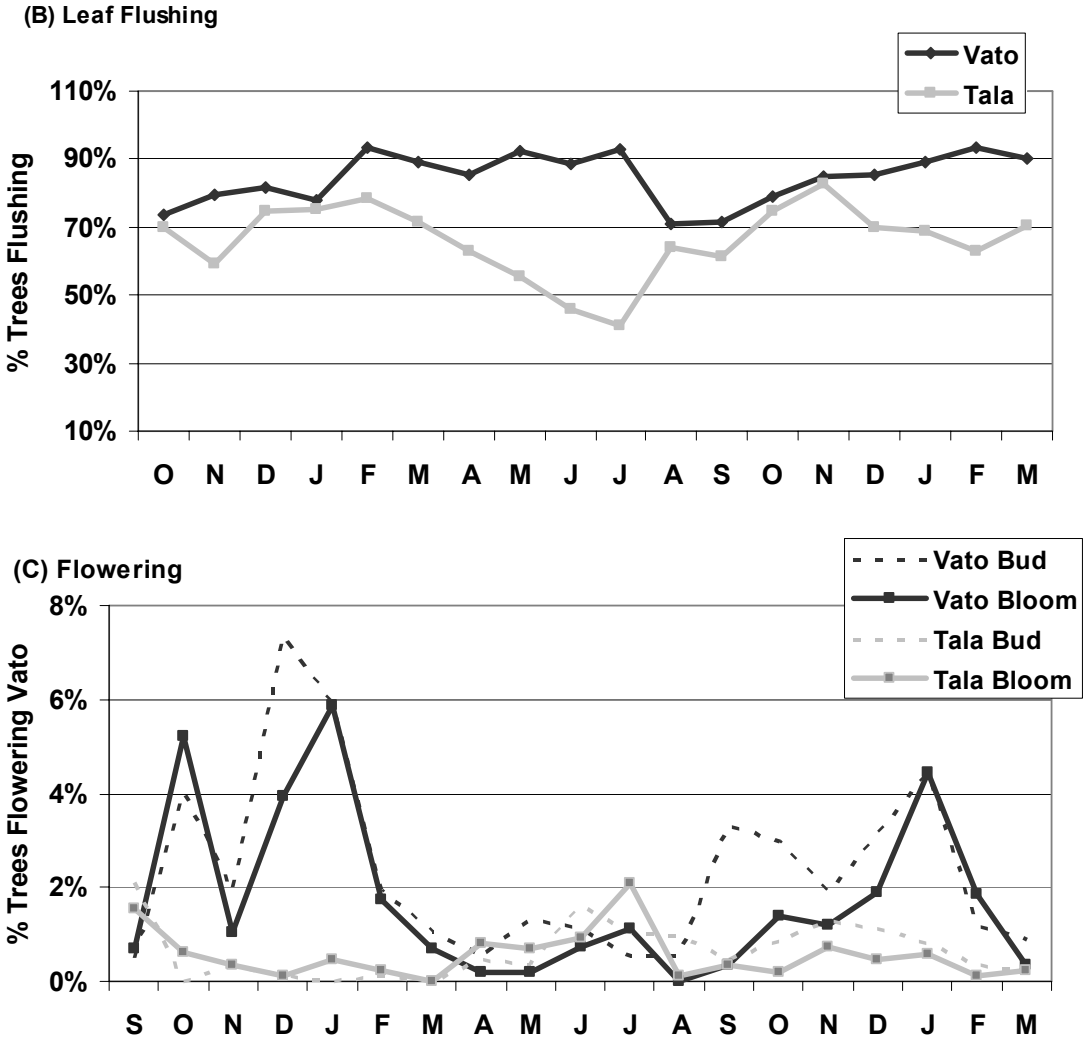


Figure 2.9. Timing of (A) fruiting, (B) leaf flushing, and (C) flowering across sites. In plot A Talatakely (gray) is on the right axis and Vatoharanana (black) is on the left axis. September is excluded from plot B.

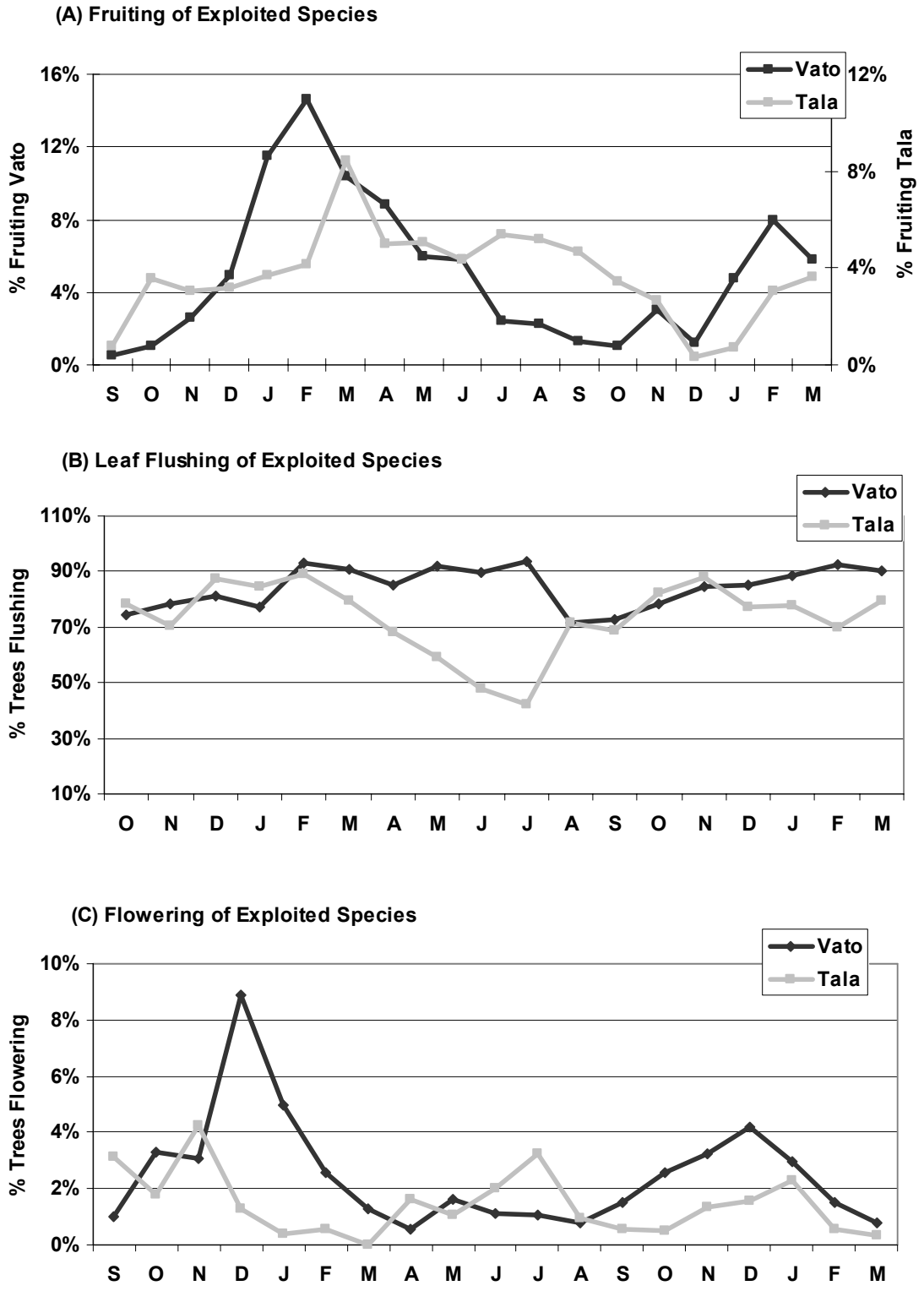


Figure 2.10. Timing of (A) fruiting, (B) leaf flushing, and (C) flowering of species exploited by *Eulemur rubriventer* (Dataset 2). In plot A, Talatakely (gray) is on the right axis and Vatoharanana (black) is on the left axis. September is excluded from plot B.

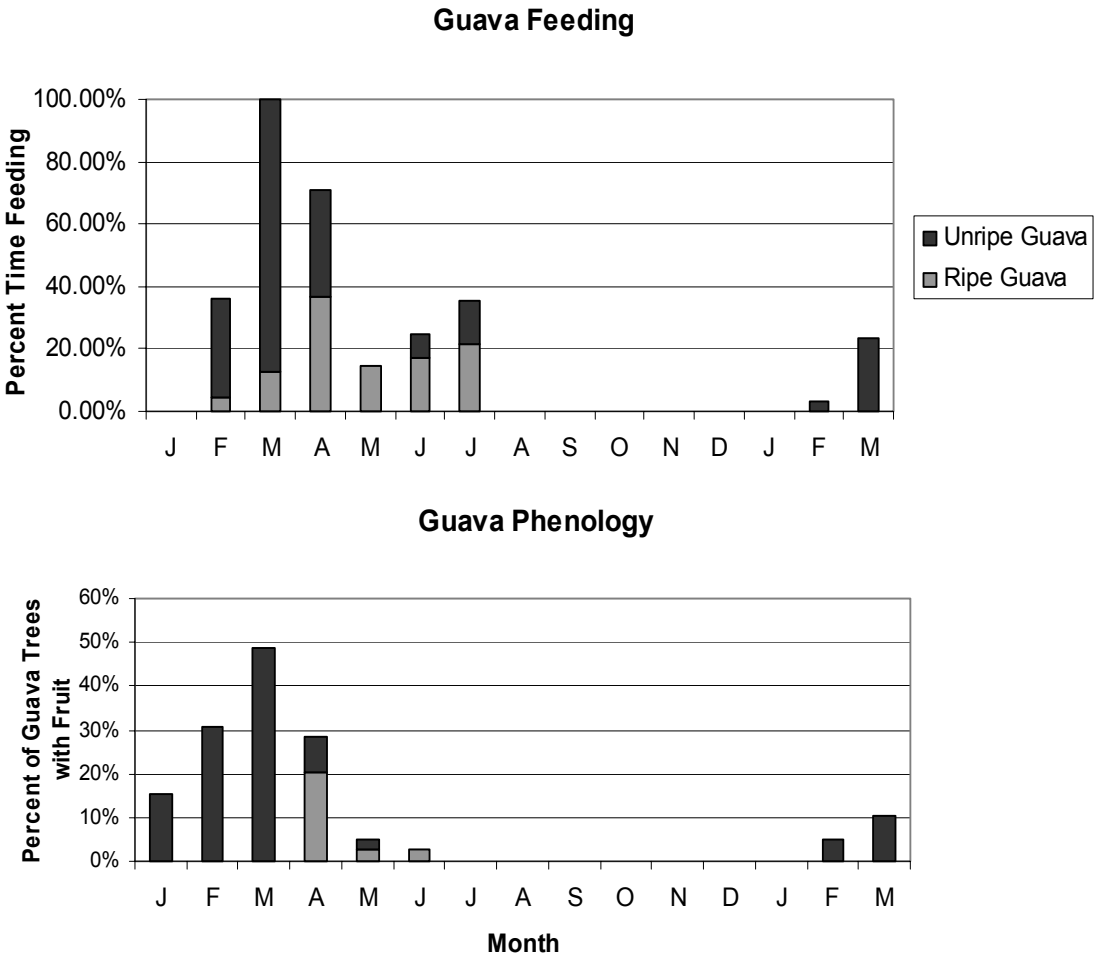


Figure 2.11. Monthly percent of time feeding of *Psidium cattleianum,* guava, in Talatakely by *Eulemur rubriventer*.

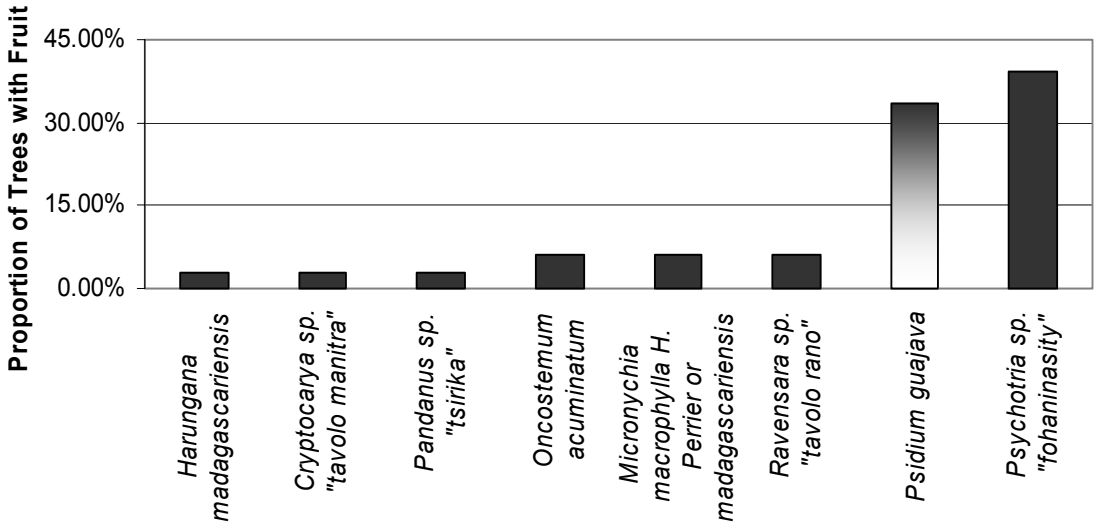


Figure 2.12. Species distribution of fruit availability in March, 2004 in Talatakely. Species not listed were not fruiting. Guava is highlighted.

Table 2.10. Leaf flushing species during peak flushing months at each site. (A) Talatakely (November 2004); (B) Vatoharanana (February 2004).. Numbers of trees in botanical plots with new leaves are listed by species with percentage of contribution for each species.

(A)

Family	Species	Vernacular	Number Trees	%	Part Eaten ?
Rubiaceae	*Psychotria sp.* "fohaninasity"	Fohaninasity	69	8.79%	No
Apocynacaeae	*Mascarenhasia arborescens*	Herodrano	59	7.52%	No
Monimiaceae	*Tambourissa thouvenotii*	Kibilany/ Ambora	43	5.48%	No
Myrtaceae	*Psidium cattleianum*	Goavy	39	4.97%	No
Myrsinaceae	*Oncostemon sp.* "kalafambakaka"	Kalafambakaka	38	4.84%	**Yes**
			248	**31.60%**	

(B)

Family	Species	Vernacular	Number Trees	%	Part Eaten?
Rubiaceae	*Psychotria sp.* "fohaninasity"	Fohaninasity	38	6.60%	No
Myrsinaceae	*Oncostemon sp.* "kalafambakaka"	Kalafambakaka	35	6.08%	**Yes**
Rubiaceae	*Psychotria* sp. "ranjopody"	Ranjopody	26	4.51%	No
Myrtaceae	*Syzygium* sp.	Rotra Fotsy	24	4.17%	No
Apocynaceae	*Carissa macrophylla*	Vangindambo	17	2.95%	No
			140	**24.31%**	

Table 2.11. Flowering species during peak flowering months at each site. (A) Talatakely (June/July 2004); (B) Vatoharanana (December/January 2004). Numbers of trees in botanical plots with flower blooms or buds are listed by species with percentage of contribution for each species.

(A)

Family	Species	Vernacular	Number Trees	%	Part Eaten?
Cunoniaceae	*Weinmannia sp.* "maka"	Maka	26	72.22%	**Yes**
Sterculiaceae	*Dombeya sp.* "merika"	Merika	4	11.11%	No
Rubiaceae	*Psychotria sp.* "fohaninasity"	Fohaninasity	2	5.56%	No
Araliaceae	*Polyscias sp.* "maniny"	Maniny	1	2.78%	No
Rubiaceae	*Gaertnera sp.* "bararata"	Bararata	1	2.78%	No
Pteridophyta	*Cyathea sp.*	Faho	1	2.78%	No
		Sehana	1	2.78%	No
		Total	**36**		

(B)

Family	Species	Vernacular	Number Trees	%	Part Eaten?
Rubiaceae	*Psychotria sp.* "fohaninasity"	Fohaninasity	34	44.16%	No
Rubiaceae	*Psychotria sp.* "ranjopody"	Ranjopody	19	24.68%	No
Oleaceae	*Noronhia sp.*	Solaitra	5	6.49%	No
Rubiaceae	*Gaertnera sp.* "bararata"	Bararata	3	3.90%	No
Myrsinaceae	*Oncostemum acuminatum*	Kalafambakaka	3	3.90%	**Yes**
Mendonciaceae	*Mendoncia couvanii* (liana)	Vahivoraka	2	2.60%	**Yes**
Arecaceae	*Neodypsis sp.* "sira"	Sira	2	2.60%	No
Rubiaceae	*Canthium sp.*Baker	Fatsikahitra	2	2.60%	No
Ebenaceae	*Diospyros gracilipes* Hiern	Hazomainty	1	1.30%	No
Cunoniaceae	*Weinmannia sp.* "maka"	Maka	1	1.30%	No
Erythroxylaceae	*Erythroxylum sp.* "malambovony"	Malambovony	1	1.30%	No
Monimiaceae	*Tambourissa sp.*	Tambonetra	1	1.30%	No
	Spec. indet. "vangindambo"	Vangindambo	1	1.30%	No
Lauraceae	*Ocotea sp. "*varongy"	Varongy	1	1.30%	No
Combretaceae	*Terminalia tetranora*	Veso	1	1.30%	No
		Total	**77**		

Phenological synchrony

Synchrony of leaf, fruit, and inflorescence production was assessed in 934 individuals from 84 species in Talatakely and 561 individuals from 76 species in Vatoharanana. The synchrony of each phenological stage varied greatly among species and the seasonality of one stage was not related to whether other stages were seasonal, uniform, or random (Table 2.12ab). Overall, species in Vatoharanana were slightly more synchronous (clumped) than species in Talatakely. A score above 1 indicates synchrony/seasonality: in Talatakely the coefficient of dispersion was significant for seasonal leaf flushing (CD = 15.57) and flowering (CD = 8.84), but not fruiting (CD = 1.78), though fruiting in 69.57% of species had CDs greater than 1 (Table 2.12a and Figure 2.13); in Vatoharanana the coefficient of dispersion was significant for seasonal leafing (CD = 11.76), fruiting (CD = 10.74), and flowering (CD = 13.58) (Table 2.12b and Figure 2.14). These results indicate higher productivity in Vatoharanana. The percentages of species in which fruiting events were (1) equal to 1 (Tala: 31.03%; Vato: 26.09%) and (2) less than 1 (Tala: 20.69%; Vato: 21.74%) were similar across sites.

The most seasonal phenophase in both sites was flowering, and the most seasonal species in Talatakely were *Weinmannia bojeriana* (Maka, flowers), *Tambourissa sp.* "kibilany" (Kibilany, flowers), and *Psidium cattleianum* (Guava, flowers) with significant CD scores ranging from 18.63 to 10.00, respectively. Of these, the flowers of *Weinmannia bojeriana* were exploited by *Eulemur rubriventer* (Table 2.12a). The most seasonal species in Vatoharanana were *Psychotria sp.* "ranjopody" (Ranjopody, flowers), *Tabernaemontana sp.* "vangindambo" (Vangindambo, flowers), and *Psychotria sp.* "fohaninasity" (Fohaninasity, fruit and flowers), with significant CD scores ranging

between 22.12 and 14.85, respectively. Of these, the fruits and flowers of *Psychotria sp.* "fohaninasity" were exploited by *Eulemur rubriventer* (Table 2.12b).

To characterize the diet of *Eulemur rubriventer,* a subset of exploited plant species ($n_{Talatakely}$ = 48 spp., 607 individuals; $n_{Vatoharanana}$ = 51 spp., 391 individuals) was analyzed (referred to hereafter as Dataset 2) (Figures 2.15 and 2.16). Dataset 2 was further analyzed by species exploited specifically for each phenological stage. CDs of species exploited for leaves, fruits, and inflorescences are indicated by the shaded areas in Figures 2.15 and 2.16. Unfortunately no CDs for exploited inflorescences are indicated for Talatakely (Figure 2.15). Two species from which *Eulemur rubriventer* ate flowers or drank nectar were present in these botanical plots and were excluded from this analysis because only 1 representative of the species was present in the plots (and therefore CDs could not be calculated). Similarly, of those species exploited for fruit, 20 species in Talatakely Dataset 2 and 21 species in Vatoharanana Dataset 2 were excluded. From these data it appears that synchrony alone did not determine whether certain species were chosen over others for food.

The distributions of CDs for new leaves and fruits of exploited foods were dissimilar across sites. For instance, lemurs in Talatakely exploited fruit from less synchronous resources and more uniformly distributed resources than lemurs in Vatoharanana. In Talatakely 0% of all species exploited for fruit had significant seasonal distributions (Figure 2.15), compared with 17% in Vatoharanana (Figure 2.16). No CDs were significantly uniform, though 20.69% had CDs less than 1 in Talatakely, compared with 13.04% in Vatoharanana. These results agree with those above in which fruit production peaks were more evident in Vatoharanana (Figure 2.10A), and indicate that

lemurs in Talatakely exploit more unpredictable fruit resources than lemurs in Vatoharana.

The dispersion of leafing was similar in each site, and only 1 of 9 (Talatakely) and 1 of 8 (Vatoharanana) species were significantly seasonal (Figures 2.15 and 2.16). These results are similar to those above, in which leaf flushing did not display clear peaks of productivity in Vatoharanana. However, results for Talatakely are perplexing since flushing did appear to be seasonal in that site (Figure 2.10b). Although no data are available for flowering in Talatakely, 100% of species from which inflourescences were exploited had CDs above 1 in Vatoharanana. 42.86% of these were significantly seasonal (Figure 2.16), as was seen above with very clear peaks in inflourescence productivity (Figure 2.10c).

Table 2.12. Phenological synchrony in each site. Coefficients of dispersion (CD) indicate level of synchrony in each species in (A) Talatakely and (B)Vatoharanana.

(A)

				New Leaves		Fruits		Inflorescences	
Family	**Species**	**Vernacular[1]**	**N[2]**	**Events**	**CD[3]**	**Events**	**CD[3]**	**Events**	**CD[3]**
Rubiaceae	*Psychotria* sp. "fohaninasity"	**Fohaninasity**	**77**	1074	4.08*	39	**1.05**	58	2.71*
Cyatheaceae	*Cyathea* sp. "faho"	Faho	62	195	6.49*	32	1.19	1	1.00
Apocynaceae	*Mascarenhasia arborescens* A. DC.	**Herodrano**	**61**	830	4.96*	25	1.86	5	**3.31***
Monimiaceae	*Tambourissa* sp. "kibilany"	Kibilany	**45**	674	1.89	6	1.78	31	13.57*
Myrsinaceae	*Oncostemum acuminatum*	**Kalafambakaka**	44	577	**1.71**	19	**0.78**	5	1.62
Myrtaceae	*Psidium cattleianum*	**Goavy**	**39**	648	1.39	14	**1.48**	10	10.00*
Lauraceae	*Cryptocarya* sp. "acuminata"	**Tavolo malady**	33	287	2.21*	20	**0.79**	0	
Monimiaceae	*Tambourissa thouvenotii*	**Ambora**	**29**	339	**1.28**	4	1.36	5	1.62
Clusiaceae/ Guttiferaceae	*Calophyllum* sp. "vitanona"	Vitanona	28	258	2.78*	4	1.36	0	
Moraceae	*Streblus dimepate* (Bureau) C.C. Berg	**Mahanoro**	26	349	1.28	7	**0.97**	2	2.00
Cunoniaceae	*Weinmannia bojeriana* Tul.	**Maka**	**26**	414	1.74	15	1.91	42	**18.63***
Lauraceae	*Ravensara* sp. "tavolo rano"	**Tavolo rano**	**22**	214	1.56	33	**1.65**	3	1.59
Clusiaceae/Guttiferaceae	*Garcinia tsaratananae*	Kimbaletaka	18	162	1.13	7	1.27	0	
Myrtaceae	*Syzygium* sp. "rotra fotsy"	**Rotra fotsy**	16	206	0.36	8	**0.88**	2	2.00
Anacardiaceae	*Micronychia macrophylla* H. Perrier or *madagascariensis*	**Sehana**	15	106	1.72	2	**0.94**	9	3.60*
Araliaceae	*Polyscias* sp. "maniny"	Maniny	**15**	90	1.19	2	2.00	9	1.73
Euphorbiaceae	*Macaranga* sp. "mokoranana"	Mokoranana	14	195	0.36	4	0.83	2	0.94
	spec. indet. "vahitamboro"	**Vahitamboro**	14	30	**2.08***	1	**1.00**	0	
Araliaceae	*Schefflera vantsilana* (Baker) Bernardi	Vantsilana	14	177	0.61	16	1.35	0	
Leguminosae	*Dalbergia baroni* Baker	Voamboana	13	165	1.20	2	0.94	0	
Rubiaceae	*Gaertnera* sp. "bararata"	**Bararata**	13	169	0.52	2	**0.94**	5	1.62
Rubiaceae	*Alberta humblotii* Drake	**Fatsikahitra**	12	133	1.05	0	**N/A**	4	1.36
Lauraceae	*Cryptocarya* sp. "tavolo manitra"	**Tavolo manitra**	11	157	0.60	12	**1.09**	0	
Myrtaceae	*Syzygium* sp. "rotra mena"	**Rotra mena**	11	153	0.39	0	**N/A**	0	
Lauraceae	*Cryptocarya* cf. *"flavescens"*	**Tavolo maintso**	10	106	0.64	6	**1.78**	0	
Sterculiaceae	*Dombeya merika*	Merika	10	148	0.56	7	0.67	6	3.19*
Oleaceae	*Noronhia* sp. "solaitra"	**Solaitra**	10	89	1.33	1	**1.00**	0	
Myrtaceae	*Syzygium* sp. "rotra"	**Rotra**	10	133	0.51	0	**N/A**	1	1.00
Rutaceae	*Zanthoxylum thouvenotii* H. Perrier	Fahavalonkazo	10	99	0.84	7	0.67	1	1.00

Tiliaceae	*Grewia* sp. "hafipotsy"	**Hafipotsy**	9	97	0.61	4	**1.36**	0	
Rubiaceae	*Mussaenda erectiloba*	**Fatora**	9	141	0.36	4	**1.89**	1	1.00
Smilaceae	*Smilex anceps* Wildenow	**Roindambo**	9	6	1.11	6	**1.43**	0	
Melastomataceae	*Dechaetanthera cordifolia* Baker	Tsingotroka (tsitrotroka)	8	108	0.70	1	1.00	7	2.78*
Ebenaceae	*Diospyros gracilipes* Hiern	Hazomainty/ Mandravalanonana	7	74	0.88	0		1	1.00
Rubiaceae	*Gaertnera* sp. "hazotoho"	**Hazotoho**	7	116	0.23*	14	**1.03**	16	3.20*
Aquifoliaceae	*Ilex mitis* (L.) Radlk.	Hazondrano	7	101	0.29*	9	1.02	1	1.00
Apocynaceae	*Landolphia* sp. "vahiherotra"	**Vahiherotra**	7	13	**1.65**	0	**N/A**	0	
Sapindaceae	*Neotina coursii* Capuron	**Lanary madinka**	7	83	0.84	3	**1.59**	0	
Lauraceae	*Ocotea* sp. "varongy vaza"	**Varongy vaza**	7	99	0.46	0	**N/A**	0	
Flacourtiaceae	*Aphloia theaeformis* Bennett	**Fandramanana**	6	89	0.29*	1	**1.00**	0	
Moraceae	*Ficus* sp. "famakilela"	**Famakilela**	6	56	**0.85**	0	**N/A**	0	
Meliaceae	*Malleastrum* sp. "tongombivy"	**Tongombivy**	6	69	0.56	11	**0.83**	1	1.00
Mendonciaceae	*Mendoncia couvanii* Vell ex Vand	**Vahivoraka**	6	3	0.33*	1	**1.00**	0	
Lauraceae	*Ocotea* sp. "varongy mainty"	Varongy mainty	6	60	0.85	0		0	
Piperaceae	*Piper pyrifolium*	Sakarivovahy	6	9	1.30	0		0	
Fabaceae	*Strongylodon craveniae*	**Vahimberana**	6	6	**0.40**	1	**1.00**	4	4.00*
Tiliaceae	*Grewia* sp. "hafitra taikalalao"	**Hafitra taikalalao**	5	80	0.09*	0	**N/A**	2	2.00
Elaeocarpaceae	*Sloanea rhodantha* var. *rhodantha* (Baker) Capuron	Vanana	5	71	0.34*	0		0	
Cunoniaceae	*Weinmannia rutenbergii* Engl.	Lalona	5	89	0.12*	5	1.62	6	2.83*
Cunoniaceae	*Weinmannia* sp. "tsisitra"	Tsisitra	5	35	1.10	1	1.00	0	
Loganiaceae	*Anthocleista madagascariensis*	Dendemy	4	34	1.03	0		0	
Vitaceae	*Cissus* sp. "vahirano"	**Vahirano**	4	3	1.00	0	**N/A**	0	
Lauraceae	*Cryptocarya* sp. "tavolo"	**Tavolo**	4	50	0.15*	0	**N/A**	0	
Loganiaceae	*Nuxia capitata,* Baker or *verticillata*, Lamark	**Lambinana**	4	70	0.09*	3	**1.59**	2	2.00
Pittosporaceae	*Pittosporum* sp. "ambovitsika"	Ambovitsika	4	52	0.24*	4	0.83	0	
Apocynaceae/Rubiaceae	*Plectaneia stenophylla* Jumelli/ *Paederia* sp. "vahiambaniakondro"	Vahiambaniakondro	4	6	0.67	15	0.50	0	
Leguminosae	*Albizia* sp. "albizia"	Albizia	3	41	0.53	5	1.20	0	
Sapindaceae	*Allophylus cobbe, macrocarpus* Danguy and Choux, or *pinnatus*	**Dikana**	3	37	**0.43**	0	**N/A**	0	
Euphorbiaceae	*Bridelia tulasneana*	Harina	3	34	0.43	0		0	

Dichapetalaceae	*Dichapetalum leucosia*	**Voandavenona**	3	8	0.81	0	**N/A**	0	
Agavaceae	*Dracaena* sp. "hasina"	Hasina	3	13	0.66	7	1.27	0	
Erythroxylaceae	*Erythroxylum* sp. "malambovony"	Malambovony	3	28	0.56	0		0	
Moraceae	*Ficus* sp. "famakilela gf"	Famakilela gf	3	34	0.35*	2	0.94	0	
Myrsinaceae	*Oncostemum* sp. "kalafambakaka gf"	**Kalafambakaka gf**	3	36	**0.46**	0	**N/A**	1	1.00
Sapindaceae	*Plagioscyphus louvelii* Danguy & Choux	Lanary mainty	3	23	0.51	1	1.00	0	
Lauraceae	*Potameia chartacea* Kosterm.	**Sary**	3	30	0.59	4	**1.36**	1	1.00
Rubiaceae	*Psychotria* sp. "ranjopody"	Ranjopody	3	48	0.19*	0		1	1.00
Rubiaceae	*Alberta* sp. "fatsikahitra pf"	Fatsikahitra (pf)	2	26	0.26*	0		2	2.00
Annonaceae	*Ambavia macrophylla* or *capuronii* (Cavaco and Keraudren) Le Thomas	Ramiavotoloho	2	18	0.41	0		0	
Burseraceae	*Canarium madagascariense* Engler	Ramy	2	18	0.17*	5	1.20	0	
Rutaceae	*Citrus aurantifolia*	Voangy	2	34	0.10*	1	1.00	0	
Lauraceae	*Cryptocarya crassifolia* Baker	Tavolo zahana	2	25	0.17*	9	1.02	0	
Moraceae	*Ficus rubra* Vahl	**Nonoka**	2	8	0.13*	4	**1.36**	0	
Clusiaceae/Guttiferaceae	*Mammea* "angustifolia var. pseudoprotorhus"	**Nato voraka**	2	20	0.47	0	**N/A**	0	
Myrsinaceae	*Oncostemum botryoides* Baker	**Kalafana**	2	23	**0.33**	2	**0.94**	0	**N/A**
Pandanaceae	*Pandanus* sp. "tsirika"	**Tsirika**	2	11	1.02	0	**N/A**	0	
Anacardiaceae	*Protorhus* sp. "sandramy"	**Sandramy**	2	30	0.21*	4	**0.83**	0	
Euphorbiaceae	spec. indet. "fanorafa gf"	Fanorafa gf	2	27	0.18*	0		0	
Euphorbiaceae	spec. indet. "fanorafa"	**Fanorafa**	2	31	0.19*	1	**1.00**	0	
Moraceae	*Treculia africana*	Apaliala/ Apaly nala	2	24	0.44	0		0	
Rutaceae	*Vepris* sp. "apodisosona"	**Apodisosona**	2	26	0.42	10	**1.56**	0	
Annonaceae	*Xylopia* sp. "ramiavona"	Ramiavona	2	28	0.33*	0		0	
	spec. indet. "sena"	**Sena**	2	26	0.26*	0	**N/A**	2	2.00
	TOTAL COMMUNITY		972	10423	15.57*	431	1.78	249	7.84*

[1]Species consumed by *Eulemur rubriventer* during the study are bolded.
[2]Sample size (N) is bolded when all three phenophases are clumped.
[3] CD of 1 indicates a uniform pattern; >1 indicates a clumped or seasonal pattern; <1 indicates a random pattern. CD asterisks (*) indicate significant departure from a Poisson distribution. Specific food items consumed by *Eulemur rubriventer* during the study are bolded. N/A is listed in bold when food items were eaten but no 'events' occurred, so insufficient data are available to calculate a CD.

(B)

				New Leaves		Fruits		Inflorescences	
Family	**Species**	**Vernacular**[1]	**N**[2]	**Events**	**CD**[3]	**Events**	**CD**[3]	**Events**	**CD**[3]
Rubiaceae	*Psychotria* sp. "fohaninasity"	**Fohaninasity**	**44**	801	2.14*	165	**15.15***	104	**14.85***
Myrsinaceae	*Oncostemum* sp. "kalafambakaka pf"	**Kalafambakaka pf**	**43**	957	**2.85***	65	**5.60***	12	3.56*
Rubiaceae	*Psychotria* sp. "ranjopody"	Ranjopody	**32**	550	3.73*	129	7.05*	82	22.12*
Myrtaceae	*Syzygium* sp. "rotra fotsy"	**Rotra fotsy**	27	483	2.31*	1	**1.00**	0	
Myrtaceae	*Syzygium* sp. "rotra mena"	**Rotra mena**	19	322	1.16	0	**N/A**	0	
Apocynaceae	*Tabernaemontana* sp. "vangindambo"	Vangindambo	**18**	401	3.30*	35	7.50*	53	20.46*
Monimiaceae	*Tambourissa thouvenotii*	**Ambora**	17	402	**1.52**	5	0.78	2	2.00
Loranthaceae	*Bakarella* sp. "tongolahy"	**Tongolahy**	**13**	109	1.40	13	**1.47**	7	2.78*
Leguminosae	*Dalbergia baroni* Baker	Voamboana	13	252	1.72	0		1	1.00
Lauraceae	*Cryptocarya* sp. "acuminata"	Tavolo malady	12	228	1.30	10	2.19*	0	
Rubiaceae	*Alberta* sp. "fatsikahitra pf"	**Fatsikahitra pf**	11	202	0.55	7	**1.27**	1	1.00
Oleaceae	*Noronhia* sp. "solaitra fotsy pf"	**Solaitra fotsy pf**	**11**	177	1.28	10	**1.13**	6	6.00*
Oleaceae	*Noronhia* sp. "solaitra"	**Solaitra**	11	194	0.68	3	**1.59**	13	3.42*
Ebenaceae	*Diospyros gracilipes* Hiern	Hazomainty	11	132	1.37	1	1.00	2	2.00
Sterculiaceae	*Dombeya pubecscens* (Hochr.) Arenes	**Hafidahy**	10	107	1.13	1	1.00	3	**1.59**
Myrsinaceae	*Oncostemum* sp. "kalafambakaka gf"	**Kalafambakaka gf**	10	150	**0.93**	0	**N/A**	1	**1.00**
Sapotaceae	*Chrysophyllum boivinianium (*Pierre) Baehni	**Rahiaka**	9	199	1.37	33	**4.40***	0	
Oleaceae	*Noronhia* sp. "solaitra fotsy"	**Solaitra fotsy**	8	94	0.95	24	**1.39**	2	2.00
Leguminosae	*Albizia gummifera* (J.F. Gmelin) C.A. Smith	**Albizia**	8	165	1.16	3	**1.59**	0	
Leguminosae	*Calliandra alternans* Bentham	Ambilazona	8	157	1.28	0		4	4.00*
Elaeocarpaceae	*Sloanea rhodantha* var. *rhodantha* (Baker) Capuron	**Vanana**	8	137	0.73	0	**N/A**	2	2.00
Cunoniaceae	*Weinmannia bojeriana* Tul.	Maka	8	179	0.90	6	1.43	6	2.13*
Sapindaceae	*Plagioscyphus louvelii* Danguy & Choux	Lanary mainty	7	79	0.62	0		0	
Rubiaceae	*Gaertnera* sp. "bararata gf"	Bararata gf	7	113.5	0.56	0		5	1.20
Lauraceae	*Cryptocarya cf. "flavescens"*	**Tavolo maintso**	7	127	0.78	3	**1.59**	0	
Lauraceae	*Cryptocarya* sp. "tavolo pina"	**Tavolo pina**	7	120	0.46	0	**N/A**	2	2.00
Fabaceae	*Strongylodon craveniae*	**Vahimberana**	7	54	1.30	14	**2.54***	0	

Apocynaceae	*Mascarenhasia arborescens* A. DC.	Herodrano	7	166	0.90	0		0	
Rubiaceae	*Alberta humblotii* Drake	**Fatsikahitra**	6	131	**0.30***	18	**1.11**	15	2.33*
Rubiaceae	*Alberta* sp. "fatsikahitra gf"	**Fatsikahitra gf**	6	81	1.79	0	**N/A**	0	
Lauraceae	*Cryptocarya* sp. "tavolo manitra"	**Tavolo manitra**	6	119	0.87	2	**0.94**	0	
Clusiaceae	*Mammea vatoensis*	**Nato jabo**	6	76	0.75	7	**1.57**	7	**3.38***
Moraceae	*Streblus dimepate* (Bureau) C.C. Berg	Mahanoro	5	97	0.80	0		0	
Erythroxylaceae	*Erythroxylum* sp. "malambovony"	Malambovony	5	87	0.69	2	0.94	1	1.00
Clusiaceae	*Mammea "angustifolia* var. *pseudoprotorhus"*	**Nato voraka**	5	68	1.56	0	**N/A**	0	
Burseraceae	*Canarium madagascariense* Engler	**Ramy**	5	69	0.71	0	**N/A**	0	
Araliaceae	*Schefflera* sp. "marorantsana"	**Marorantsana**	5	69	0.89	1	1.00	5	**1.62**
Anacardiaceae	*Protorhus* sp. "sandramy"	**Sandramy**	5	113	0.70	0	**N/A**	0	
Sapindaceae	*Glenniea pervillei* (Baill.)	Lanary speciale	4	85	0.53	8	0.88	9	2.43*
Rubiaceae	*Gaertnera* sp. "bararata"	**Bararata**	4	63	0.30*	1	**1.00**	4	1.36
Myrtaceae	*Syzygium* sp. "rotra"	**Rotra**	4	87	0.47	4	**1.36**	1	1.00
Moraceae	*Ficus* sp. "famakilela pf"	**Famakilela pf**	4	40.5	1.61	4	**1.36**	0	
Moraceae	*Treculia africana*	**Apaliala/ Apaly nala**	4	82	0.70	2	**0.94**	0	
Meliaceae	*Malleastrum* sp. "tongombivy"	**Tongombivy**	4	70	0.82	0	**N/A**	6	1.43
Lauraceae	*Ocotea* sp. "varongy vaza"	Varongy vaza	4	98	0.74	1	1.00	2	0.94
Asteraceae	*Vernonia* sp. "tavilona"	**Tavilona**	4	92	**0.26***	0		10	2.61*
Apocynaceae	*Landolphia* sp. "vahiherotra"	Vahiherotra	4	29	0.68	0		0	
Annonaceae	*Ambavia macrophylla* or *capuronii* (Cavaco and Keraudren) Le Thomas	**Ramiavotoloho**	4	98	0.37	0	**N/A**	0	
Anacardiaceae	*Micronychia macrophylla* H. Perrier or *madagascariensis*	**Sehana**	4	64	0.44	0	**N/A**	0	
Anacardiaceae	*Protorhus* sp. "sandramy fotsy"	**Sandramy fotsy**	4	53	0.42	0	**N/A**	0	
Anacardiaceae	*Protorhus* sp. "sandramy mena"	**Sandramy mena**	4	62	0.44	0	**N/A**	0	
Verbenaceae	*Clerodendrom petunioides*	Voalatakakoholahiala	3	23	0.60	1	1.00	3	3.00*
Sapindaceae	*Neotina coursii* Capuron	**Lanary madinka**	3	47	0.42	0	**N/A**	0	
Myrsinaceae	*Oncostemum* sp. "kalafambakaka"	**Kalafambakaka**	3	24	**0.53**	0	**N/A**	1	**1.00**
Monimiaceae	*Tambourissa parvifolia* Baker	**Ambora lahy**	3	45	**0.39**	0		0	
Monimiaceae	*Tambourissa* sp. "kibilany"	Kibilany	3	75	0.52	0		0	
Lauraceae	*Ocotea cf. racemosa* (Danguy)	Varongy fotsy	3	74	0.41	1	0.41	0	0.41

	Kosterm.								
Cyatheaceae	*Cyathea* sp. "faho"	Faho	3	6	0.72	0		0	
Combretaceae	*Terminalia tetranora*	**Veso**	3	59	**0.35**	3	0.89	4	1.89
Clusiaceae	*Garcinia tsaratananae*	**Kimbaletaka**	3	49	0.32*	0	**N/A**	0	
Clusiaceae	*Garcinia/Rheedia?* sp. "voamalambotaho"	**Voamalambotaho**	3	34	1.28	0	**N/A**	11	4.09*
Araliaceae	*Polyscias* sp. "maniny"	Maniny	3	27	1.59	0		0	
Apocynaceae	*Carissa edulis*	**Fatsy**	3	59	0.35	0	**N/A**	0	
	spec. indet. "herodambo"	Herodambo	3	58	0.53	1	1.00	1	1.00
Rutaceae	*Vepris* sp. "apody"	Apody	2	28	0.33*	0		0	
Proteaceae	*Dilobeia thouarsii* Roemer & Schultes	**Ramandriona**	2	34	0.22*	0	**N/A**	0	
Palmae/Arecaceae	*Dypsis nodifera /Neodypsis*sp. "sira hazo"	**Sira hazo**	2	34	0.16*	14	**0.43**	17	1.23
Myrtaceae	*Syzygium "emirnensis"*	**Robary**	2	46	0.57	0	**N/A**	0	
Moraceae	*Ficus botryoides* Baker	**Voara rano**	2	44	**0.39**	22	**0.60**	0	
Moraceae	*Ficus* sp. "famakilela"	**Famakilela**	2	24	0.43	0	**N/A**	0	
Mendonciaceae	*Mendoncia couvanii* Vell ex Vand	**Vahivoraka**	2	22	0.14*	1	**1.00**	9	**2.90***
Loganiaceae	*Anthocleista madagascariensis*	**Dendemy (vavy)**	2	54	0.24*	5	**1.20**	2	0.94
Fabaceae	*Abrus precatorius*	Vahimboamena	2	10	0.18*	0		2	2.00
Euphorbiaceae	*Macaranga* sp. "mokoranana"	Mokoranana	2	37	0.60	0		0	
Dichapetalaceae	*Dichapetalum leucosia*	**Voandavenona**	2	14	**0.38**	0		0	
Cunoniaceae	*Weinmannia* sp. "tsisitra"	Tsisitra	2	64.5	0.40	0		0	
Clusiaceae	*Ochrocarpus?* sp. "voasititinjaza"	Voatsititinjaza	2	38	0.33*	0		0	
Apocynaceae/ Rubiaceae	*Plectaneia stenophylla Jumelli/ Paederia* sp. "vahiambaniakondro"	Vahiambaniakondro	2	17	0.15*	0		0	
	TOTAL COMMUNITY		**590**	9937	11.76*	626	10.74*	418	13.58*

[1]Species consumed by *Eulemur rubriventer* during the study are bolded.
[2]Sample size (N) is bolded when all three phenophases are clumped.
[3] CD of 1 indicates a uniform pattern; >1 indicates a clumped or seasonal pattern; <1 indicates a random pattern. CD asterisks (*) indicate significant departure from a Poisson distribution. Specific food items consumed by *Eulemur rubriventer* during the study are bolded. N/A is listed in bold when food items were eaten but no 'events' occurred, so insufficient data are available to calculate a CD.

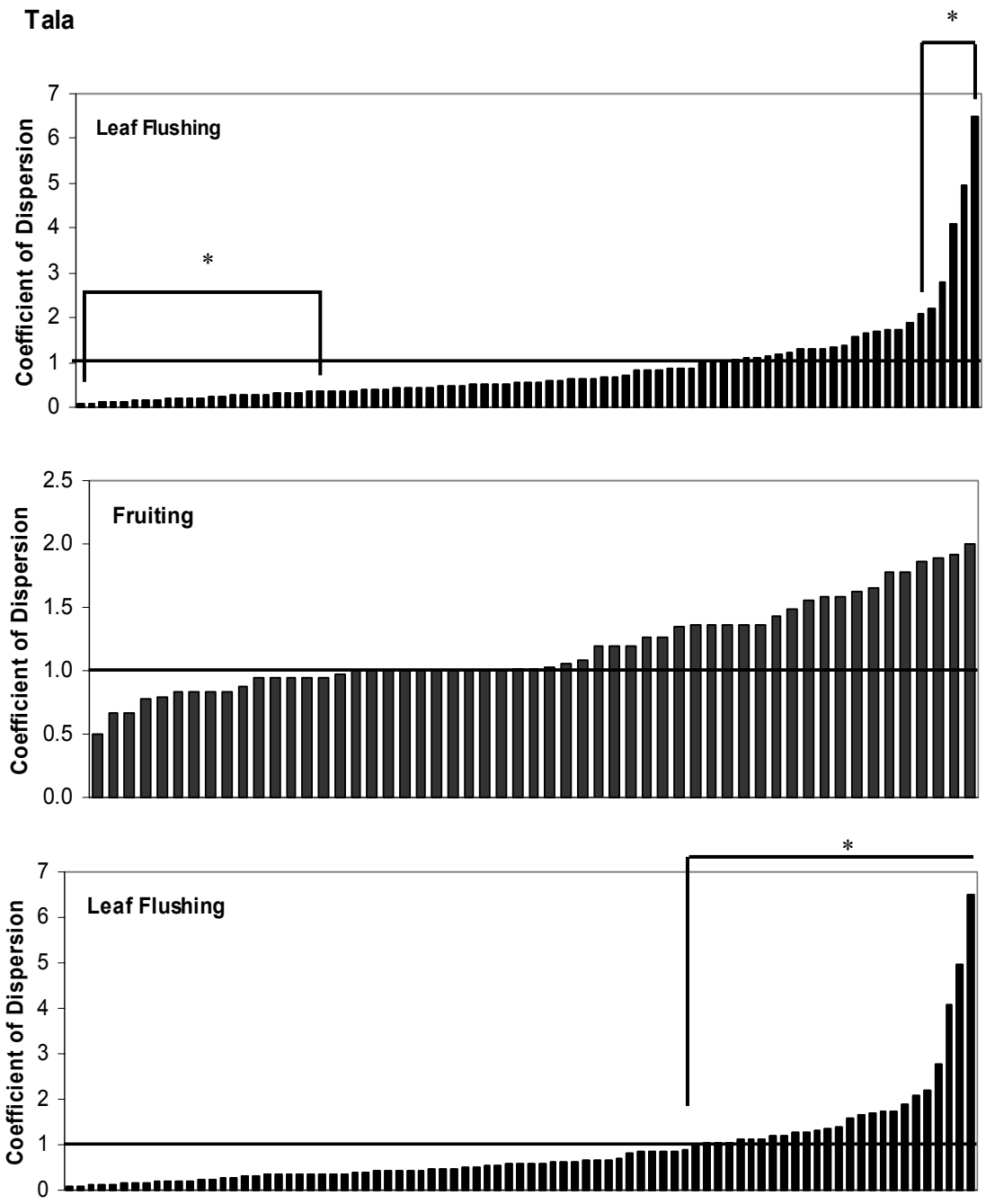


Figure 2.13. Coefficient of dispersion for plant species in Talatakely. CD of 1 indicates a uniform pattern; >1 indicates a clumped or seasonal pattern; <1 indicates a random pattern. Values of zero indicate species for which no events were recorded. Asterisks (*) indicate significant departure from a Poisson distribution.

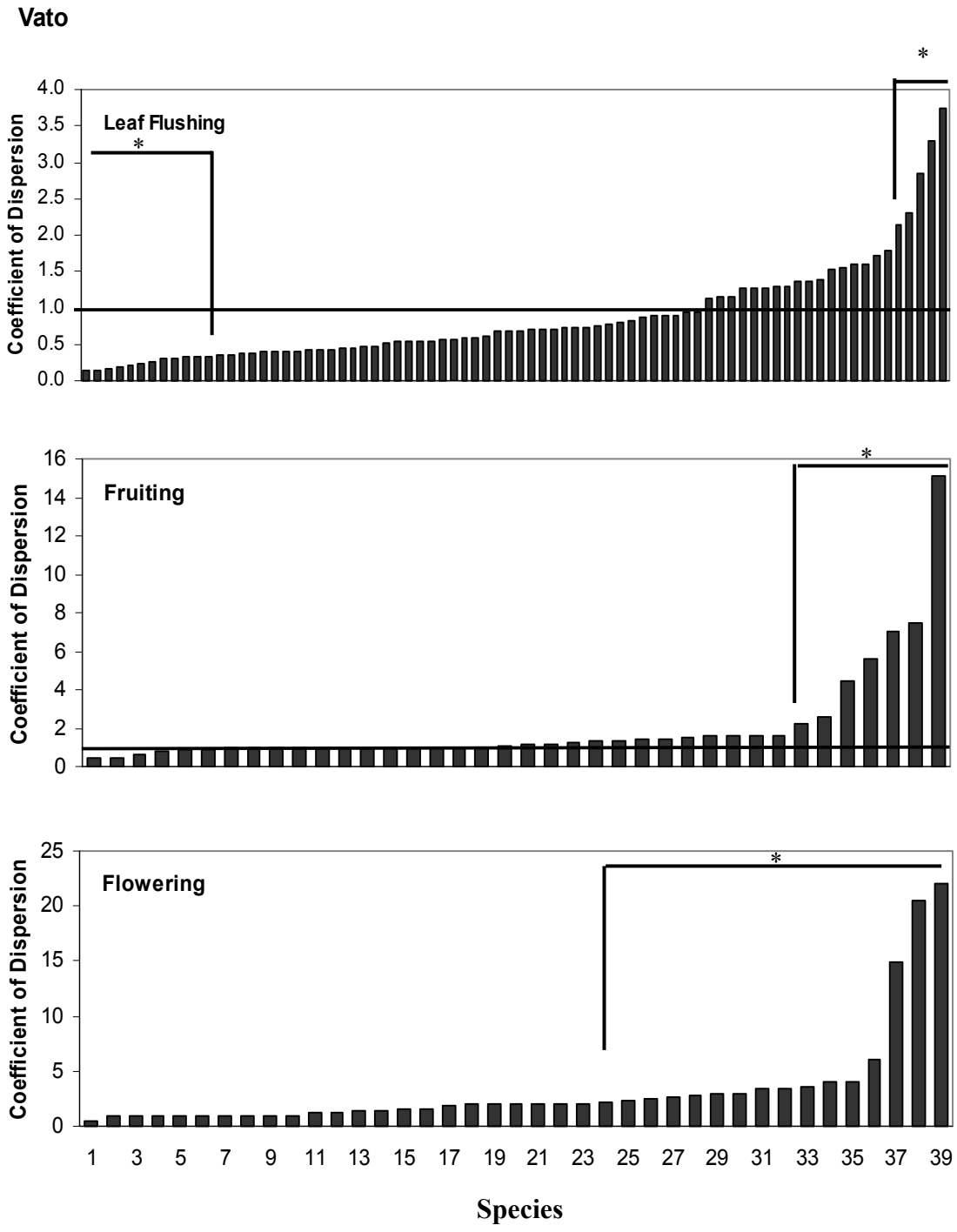


Figure 2.14. Coefficient of dispersion for plant species in Vatoharanana. CD of 1 indicates a uniform pattern; >1 indicates a clumped or seasonal pattern; <1 indicates a random pattern. Values of zero indicate species for which no events were recorded. Asterisks (*) indicate significant departure from a Poisson distribution.

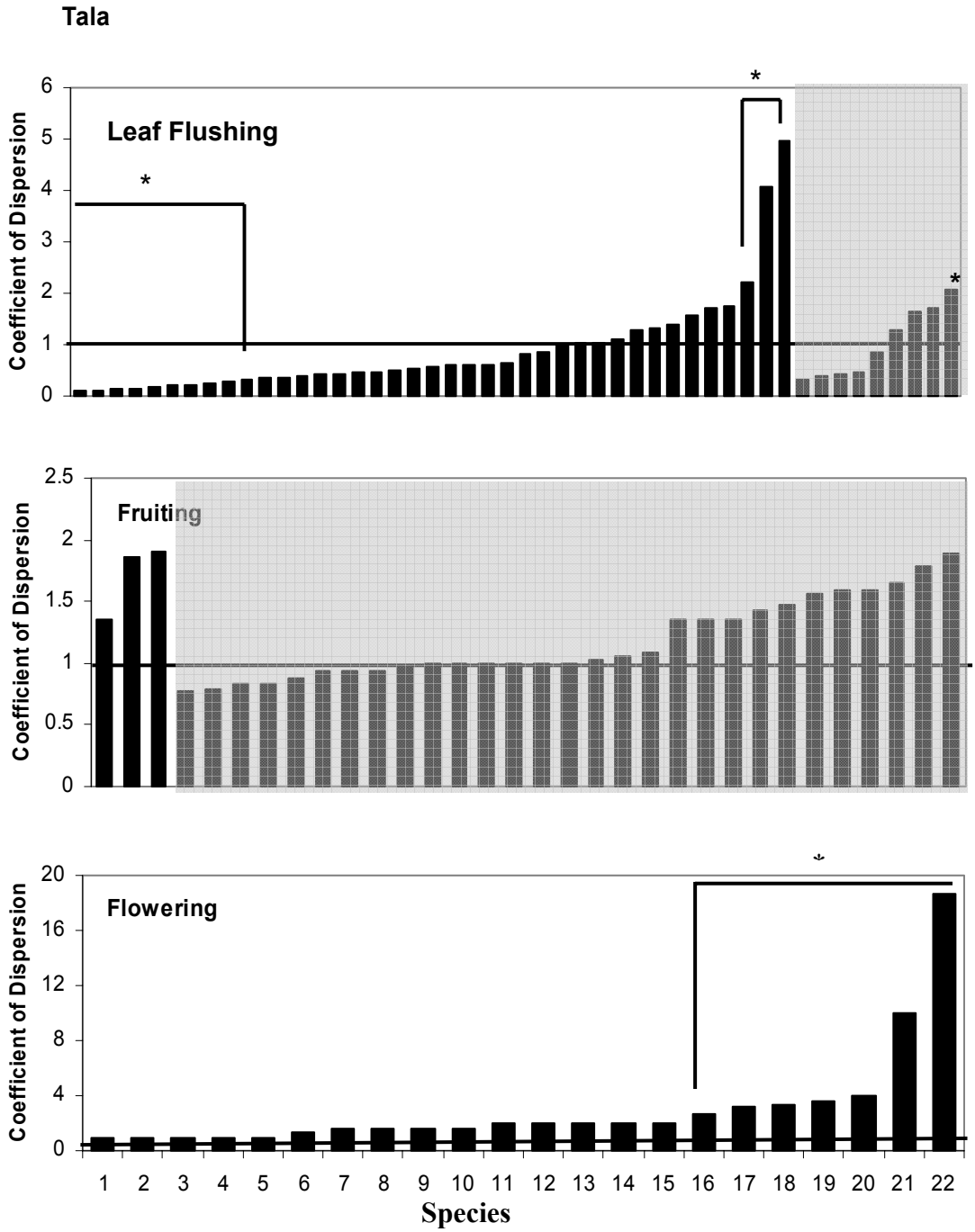


Figure 2.15. Coefficient of dispersion of exploited species in Talatakely. CD of 1 indicates a uniform dispersion; >1 indicates a clumped or seasonal dispersion; <1 indicates a random dispersion. Shaded areas indicate species which were exploited for the phenological stage indicated by the graph. None of these species were exploited for flowers. Asterisks (*) indicate significant departure from a Poisson distribution.

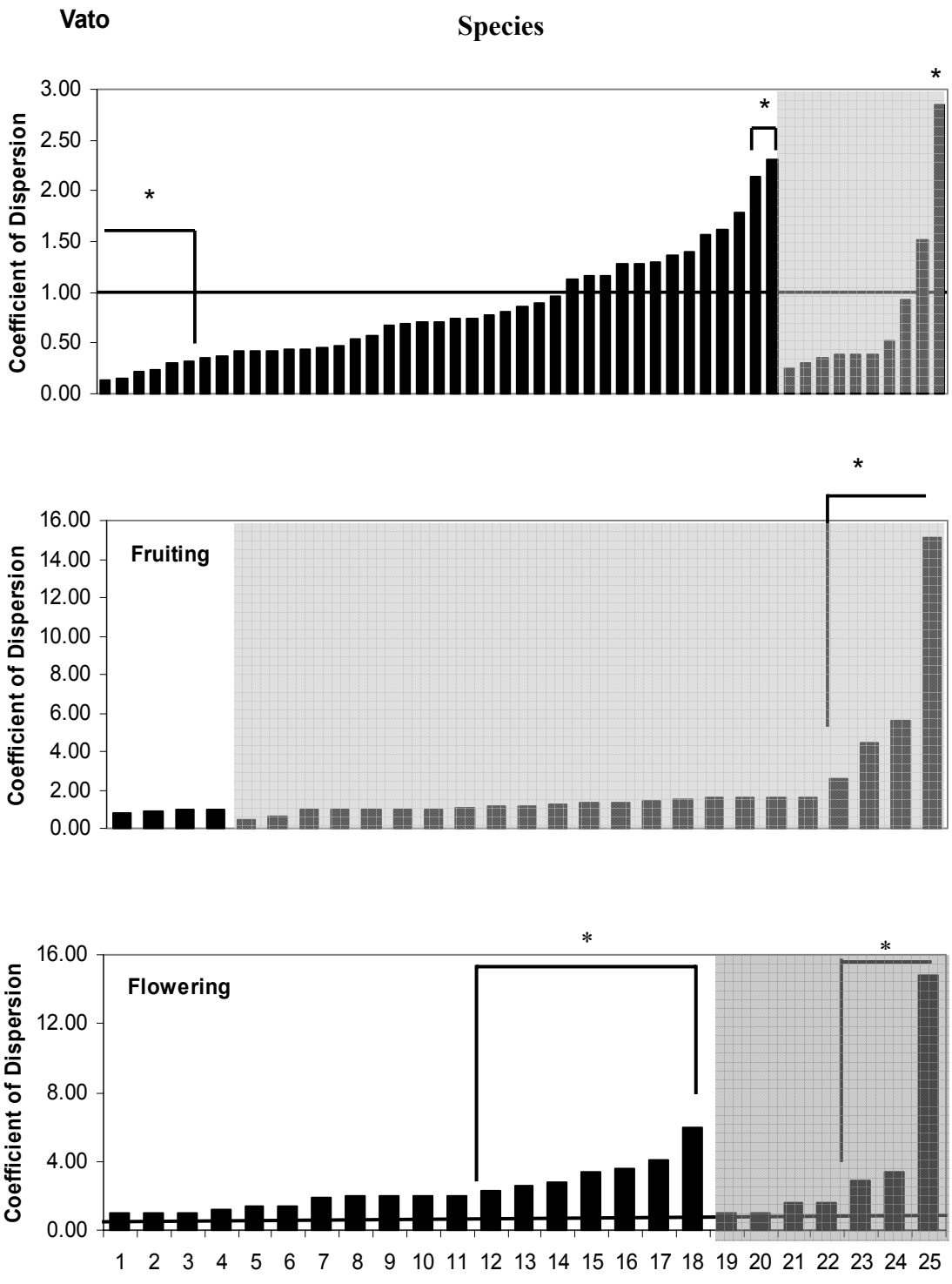


Figure 2.16. Coefficient of dispersion of exploited species in Vatoharanana. CD of 1 indicates a uniform dispersion; >1 indicates a clumped or seasonal dispersion; <1 indicates a random dispersion. Shaded areas indicate species which were exploited for the specific phenological stage indicated by the graph. Asterisks (*) indicate significant departure from a Poisson distribution.

Climate and Phenology

The correlation between relative abundance of fruiting trees and rainfall, minimum temperature, and maximum temperature was tested for each site. As rainfall was not significantly correlated with maximum temperature (see above), the relative abundance of fruiting trees was not significantly related to maximum temperature in either site (Figure 2.17). Monthly minimum temperature and relative abundance of fruiting trees were significantly negatively correlated in Talatakely, $r(16) = -0.50$, $p<.05$, and monthly rainfall and relative abundance of fruiting trees were significantly positively correlated in Vatoharanana, $r(16) = 0.61$, $p<.01$ (Figure 2.17). Both sites followed the same trend (either positively or negatively correlated) for rainfall and maximum temperature. However, relationships between minimum temperature and fruiting diverged across sites (Figure 2.17).

These analyses were further conducted using Dataset 2 for relative abundance of fruiting trees and tests yielded the same results. No significant correlations were found in Talatakely, whereas fruiting was significantly positively correlated with both rainfall, $r(18) = 0.61$, $p<.01$, and minimum temperature, $r(18) = .49$, $p<.05$, in Vatoharanana.

Leaf flushing in Talatakely was significantly positively correlated with minimum temperatures, $r(18) = 0.678$, $p<.001$, and maximum temperatures, $r(18) = .644$, $p<.001$, using both datasets (Figure 2.18). Leaf flushing in Vatoharanana was positively correlated with rainfall, $r(18) = 0.472$, $p< .05$, but flushing on species exploited was not correlated with climate (Figure 2.18).

Flowering in Talatakely was negatively correlated with minimum temperatures, $r(18) = -0.478$, $p<.05$, and maximum temperatures, $r(18) = -0.534$, $p<.05$, though flowering in exploited species was not significantly correlated with climate (Figure 2.19). Flowering in Vatoharanana was not significantly correlated with climate, although

flowers exploited were positively correlated with maximum temperature, r(18) = 0.519, $p<.05$ (Figure 2.19).

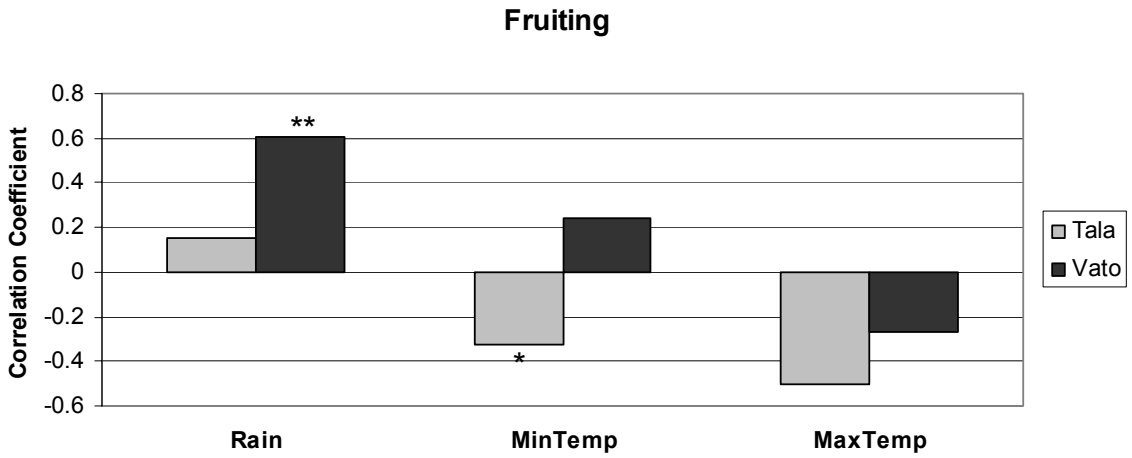


Figure 2.17. Strength of relationship between the relative abundance of fruiting trees and climate (rainfall, minimum temperature, maximum temperature). N = 18 for each site (October 2003 through March 2005).

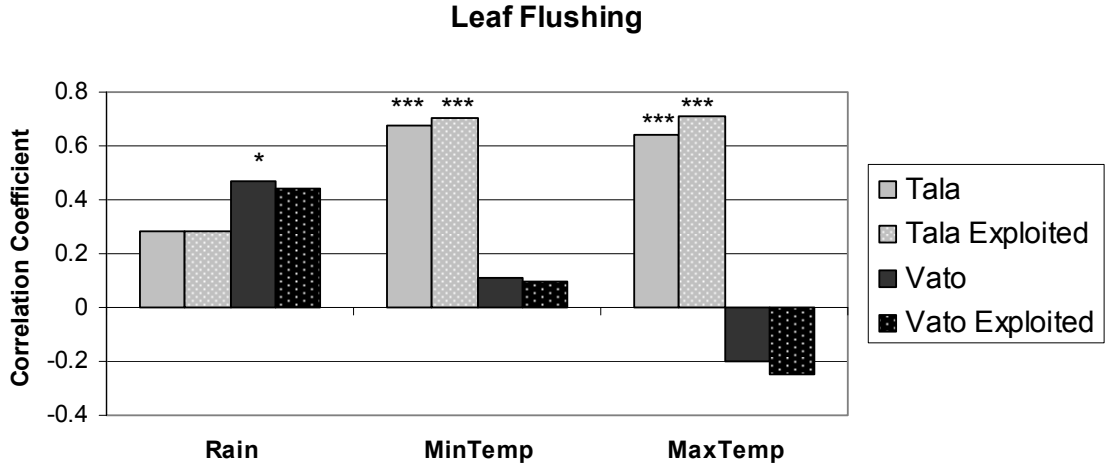


Figure 2.18. Strength of relationship between the relative abundance of trees in flush and climate (rainfall, minimum temperature, maximum temperature). N = 18 for each site (October 2003 through March 2005).

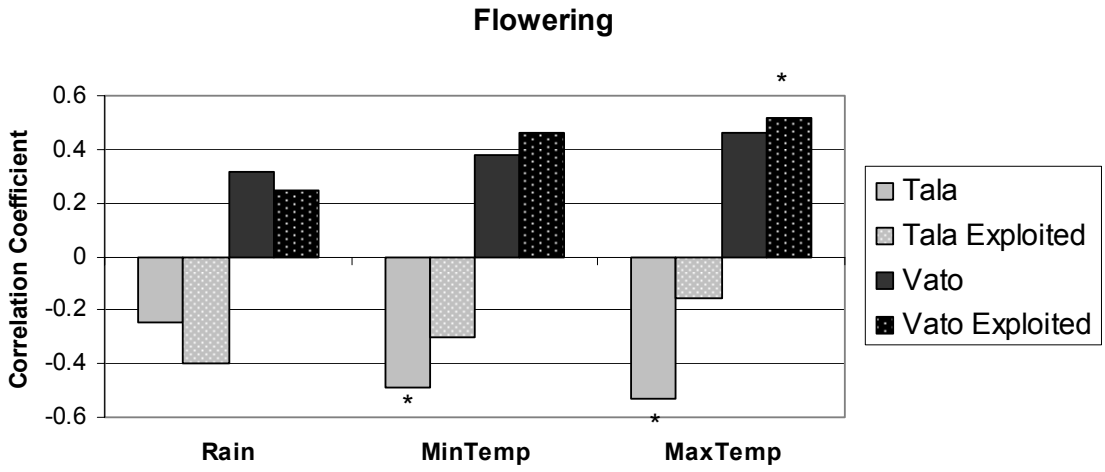


Figure 2.19. Strength of relationship between the relative abundance of flowering trees and climate (rainfall, minimum temperature, maximum temperature). N = 18 for each site (October 2003 through March 2005).

DISCUSSION

Botanical Plots

As predicted, measures of forest population and community structure and diversity indicated that forest quality was higher in the undisturbed site, Vatoharanana. These results are in large agreement with studies conducted in different microhabitats within these two sites, and strikingly similar to studies conducted earlier in the regeneration process. According to previous research and this study, Talatakely is functionally more degraded than Vatoharanana.

Forest population and community structure

Talatakely had less emergent trees, and overall smaller trees in height and DBH (Figure 2.20). These results agree with those found by several previous studies (White *et al.*, 1995; Balko, 1998; Dagosto and Yamashita, 1998; Grassi, 2001; Durham, 2003; Brown and Gurevitch, 2004; Balko and Underwood, 2005), and yield particularly similar

results if different sampling procedures are considered. Balko and Underwood (2005) report taller trees (Talatakely: 13.22 m; Vatoharanana: 15.07 m) with larger DBH (Talatakely: 19.76 cm; Vatoharanana: 31.20 cm) in both sites compared with this study. The difference between studies is most likely due to differences between the DBH of trees included for study. Balko and Underwood (2005) measured all trees >10 cm DBH, while all trees >2.5 cm were included in this study. In both studies trees located in botanical plots in Vatoharanana were taller with larger DBH. In fact, in both studies trees in Talatakely were on average 37% smaller and 11% (Balko and Underwood, 2005) to 12% (this study) shorter.

Crown depths were significantly different between sites, as was found in previous studies; but contrary to past studies, crown depths in this study were *larger* in Talatakely. Crown diameters were also larger in Talatakely, though not significantly (Figure 2.20).

Though such measurements are visually estimated and not precise, the reason for these differences between studies is unknown. However, while crown diameter was larger in Vatoharanana than in Talatakely during a study by White and colleagues (1995), they also did not find a large difference between the two sites (Crown depth Tala: $1.7m^3$; Vato: $1.8m^3$). Several years have passed since earlier studies of crown diameters in these two sites, and it is quite possible that this difference is due to growth during the interim. Balko and Underwood (2005) found that "the *impact* of selective logging in (Vatoharanana) is roughly equivalent to a removal rate that is 10 times greater than the actual number of harvested stems" (64) and a change in the spatial dispersion of trees was responsible for rapid crown expansion by trees adjacent to newly created gaps. If the same process occurred in Talatakely and more extensive extraction in that site yielded larger light gaps relative to Vatoharanana, more space may have been made available for

crown growth in that site. A more precise method of crown measurement may be warranted in future studies, though studies comparing total crown volume, a more informative measure and usually the impetus for measuring crown depth and diameter in the first place, consistently find larger and less variable crown volumes in Vatoharanana (*e.g.,* Balko, 1998; Dagosto and Yamashita, 1998; Balko and Underwood, 2005). In fact, tree crowns in Vatoharanana are less degraded than those in the adjacent pristine (unlogged) forest Valohoaka (Balko and Underwood, 2005). Microhabitat differences were found within each site, though this variation was on a much smaller scale than inter-site differences and does not detract from the validity of these differences.

Basal area/ha in Talatakely was less than half that in Vatoharanana, indicating smaller forest biomass and a less uniform distribution of individual trees (Figure 2.20). These results also agree with studies conducted previously (White *et al.*, 1995; Balko, 1998), and conform to classic ideas on the adverse impact of timber extraction on biodiversity. For instance, in Talatakely CVs of basal area/ha were larger and species evenness was lower, both of which are associated with lower tree diversity and indicate a patchy distribution of stems and human use of particular trees (Sagar and Singh, 2006).

Sampling procedures in this study differed from several previous studies in these sites (*e.g.,* Atsalis, 1999aa; Balko, 1998; Hemingway, 1998; Hemingway and Overdorff, 1999; Grassi, 2001; Balko and Underwood, 2005) in that a lower minimum tree size was set ($\geq$2.5 cm DBH) for analysis (but see Durham, 2003). When only trees 10cm DBH or larger were analyzed for direct comparison with other studies, results were largely similar (*e.g.,* trees were significantly shorter in Talatakely), but DBH site differences were no longer significant, indicating that DBH differences from the original dataset were driven by the large number of small trees in Talatakely. These findings are in agreement with

Durham (2003), who found a larger number of small diameter trees in Talatakely. Several studies conduct a sampling of trees ≥ 10 cm DBH (Williamson and Gaston, 2005), and less often ≥ 5 cm DBH (*e.g.,* Hemingway, 1998; Hemingway and Overdorff, 1999; Grassi, 2001) or even ≥ 3 cm DBH (Atsalis, 1999aa). While studies with a higher cut-off may be useful for assessing a forest's canopy (Hubbell and Foster, 1983), such analyses may exclude important species with smaller DBH (*e.g., Psidium cattleianum*) when analyzing the phenological cycling of a disturbed forest or the diet of a species, and a lower sampling threshold may be preferable. Furthermore, the DBH of canopy species in tropical forests is highly variable (Leigh, 1999). An assessment with a lower DBH cut-off enables this type of analysis as well as canopy comparisons. Utilizing both types of analyses (different size classes), this study indicates that the canopy is less developed in Talatakely, yet not significantly different than Vatoharanana.

Forest population and community diversity: taxonomic composition

While species richness was lower in the disturbed site, Talatakely (*contra* Balko, 1998), sites did not vary significantly. These results are not consistent with all previous studies in these particular sites, though they are consistent with patterns found in Ranomafana (*e.g.,* Ganzhorn *et al.,* 2003a; Brown and Gurevitch, 2004). Lower species richness with greater selective extraction is also expected if selective extraction increases the scale and importance of competition (Phillips *et al.,* 1994). Certain areas surveyed in this study would also promote such a finding since one plot contained guava (*Psidium cattleianum*), an aggressively invasive exotic species in areas that have been cleared (Brown and Gurevitch, 2004).

Several species were rare, and the majority of individuals belonged to few species in both sites, consistent with the negative skew present in most ecological communities

(Margurran and Henderson, 2003). Whether a species is rare or common is a function of its tenure (Margurran and Henderson, 2003). Yet this may not be the case in disturbed habitats where trees are selectively extracted or invasive species are introduced. Clearly this is also not the case in Talatakely where guava is both abundant and relatively young (Wright, 1992, 1997), having been introduced to this forest in 1950 (P. Wright, personal communication). However, the ensuing pattern holds: the typical distribution of species abundance in ecological communities, where dominant species are rare and rare species are common (Margurran and Henderson, 2003; Williamson and Gaston, 2005), was found in both sites. The proportion of relative dominance to relative abundance highlighted site differences, where a lower density of species were dominant in Talatakely (*cf* Balko and Underwood, 2005), an expected outcome when a large number of individuals of specific species are extracted.

Dominant species in each site differed. Of all stems greater than 10cm DBH, Maka (Cunoniaceae, *Weinmannia bojeriana*) was the relatively most dominant species present in Talatakely. This species was one of the most dominant in Talatakely between 1993 and 1994 as well (Balko and Underwood, 2005), which suggests that large-scale change has not occurred in the last decade. Maka was exploited for flowers by *Eulemur rubriventer,* though only in one month, and only in Talatakely. Rahiaka (*Chrysophyllum boivianium,* Sapotaceae) was the relatively most dominant species present in Vatoharanana. Rahiaka was exploited for fruit February through September, and heavily exploited March through August (ranging from 24-42% of feeding time per month) in Vatoharanana. In contrast, Rahiaka was only exploited in May and June in Talatakely, and to a much lesser degree (approximately 15% of feeding time each month). This divergence is likely due to variable availability among sites. No Rahiaka fruiting events

were recorded from botanical plot trees in Talatakely, indicating that Rahiaka fruiting was extremely rare in that site during this study. In Vatoharanana Rahiaka fruit feeding occurred in every month in which it was present. These results suggest that species in positions of dominance in Vatoharanana are more important food sources for *Eulemur rubriventer* than they are in Talatakely. However, longitudinal data are necessary to determine whether Maka fruiting schedules vary inter-annually, and if so how this impacts exploitation of Maka by *Eulemur rubriventer.*

13 families were located in only a single site (8 in Talatakely; 5 in Vatoharanana), and while no families unique to Talatakely were consumed by *Eulemur rubriventer,* 3 families unique to Vatoharanana were (Tecot, this study). The largest difference between the sites was the position of dominance occupied by Cyatheaceae, which was represented by one species, *Cyathea sp.* "faho" (tree fern), in Talatakely. This is not a food species for *Eulemur rubriventer* (Tecot, this study) or other large-bodied frugivores in the forest, so it is likely not a major influence on any inter-site behavioral differences. Both sites were largely dominated by Rubiaceae, Myrtaceae, and Lauraceae. Lauraceae accounted for the largest proportion of standing biomass in both sites (on both the generic and familial levels). The dominant position of Myrtaceae in both sites is notable since guava (Myrtaceae, *Psidium cattleianum*) is exclusive to Talatakely. Results for the taxonomic structure of Vatoharanana are consistent with Hemingway (1998) with the exception of the large presence of Rubiaceae. This may be accounted for in part by the fact that many trees in the Rubiaceae family are smaller than 5 cm DBH and were not sampled in her study.

Forest community diversity: diversity indices

Both indices indicated greater species and structural diversity in Vatoharanana, though not significantly. Differences were extremely minor using Simpson's diversity index, which is weighted more heavily by evenness (versus richness) than the Shannon and Wiener index. This result is likely a relic of small sample size combined with differences in microhabitat within sites. For instance, the likelihood of this particular index to yield a higher index increases as sample size decreases. Thus, the lower diversity calculated in this study for the disturbed site is a conservative estimate, and indicates that logging in this site did not increase diversity as it has in other communities (Ganzhorn, 1995b; Purvis and Hector, 2000). Low diversity following a disturbance may occur if the disturbance is short (because of the short time for immigration) and/or frequent (reducing the ability of new species to mature) (Connell, 1978). Contrary to this study and studies by Balko (1998) and Brown and Gurevitch (2004), Grassi (2001) found greater diversity in the disturbed site, though she focused upon microhabitats within *Hapalemur griseus* home ranges. High diversity in tropical rain forests is an attribute which is often the result of light gaps created by tree felling (Ganzhorn, 1995b; Purvis and Hector, 2000), and may be indicative of intermediate level disturbance (Connell, 1978), which may better characterize bamboo lemur microhabitat. This finding highlights the importance of considering the functional habitat of specific species on an appropriate scale when describing a habitat.

Climate

Predictable changes in temperature and rainfall (*i.e.,* climate seasonality) occurred (see also Atsalis, 1999aa). The cold season occurred approximately April through October and the warm season occurred approximately November through

February/March during the course of this study. Sites were very similar but the minimum and maximum temperatures in Vatoharanana reached a couple of degrees lower and higher, respectively, than temperatures Talatakely. The rainy season occurred December through March and the dry season occurred April through November. Although rainfall can vary from year to year (Dewar and Richard, 2007), the delineation of rainy and wet seasons was consistent with Atsalis (1999), who further reports that lower temperatures occurred during the dry season and highest temperatures occurred during the wet season. In this study, the cold season was dry. However, during the warm season there was more variability in rainfall, so there were effectively three climatic seasons: warm and wet (December-March), cold and dry (April-October), and warm and dry (October-December).

Phenology, Synchrony, and Food Availability Seasons

Phenological cycles were seasonal, with clear scarce and abundant seasons, as has been found in Ranomafana and other rain forest regions in Madagascar (*e.g.,* Overdorff, 1991; Morland, 1993; S. Johnson, 2002; Bollen and Donati, 2005). The more disturbed site, Talatakely, was less predictable with longer fruit scarce periods and shorter fruit abundant periods.

Site Differences

Periods of maximal scarcity of all food combined occurred April through July (cold/dry) in the disturbed site, Talatakely, while greatest scarcity occurred August through November/December (transition from cold/dry to warm/dry) in the undisturbed site, Vatoharanana (Figure 2.21). Slight shifts in the timing of the scarce season have great implications for lemur life histories: April through July coincides with pre-breeding, breeding, and early gestation, and August through November coincides with

birth and lactation in *Eulemur rubriventer*. If food is scarce and energy stores are not sufficient during the breeding season, reproduction may not be supported (see Chapters 1 and 4).

Phenological comparisons of these two sites are rare, but Grassi (2001) reported no differences in fruit or new leaf availability in these two sites. In contrast, a lower percentage of trees bore fruit, flowers, and new leaves in Talatakely than in Vatoharanana throughout this study, and overall productivity and seasonality were higher in Vatoharanana. Seasonal distributions for all phenophases in Vatoharanana were also found by Johnson (2002), though this type of analysis has not been done previously in Talatakely for comparison. As Grassi's (2001) study area was located within *Hapalemur* microhabitat, these results suggests that habitat disturbance affects *Hapalemur* and *Eulemur* resources differently.

Periods of fruit abundance appeared almost random from month to month in Talatakely, and highly seasonal in Vatoharanana. This may be due in part to unsynchronized phenological patterns between canopy and understory trees, found in several forests including Ranomafana (Hemingway and Overdorff, 1999). Although these results were found for Vatoharanana by Hemingway and Overdorff (1999), the greater number of understory trees included in the Talatakely sample may exacerbate this result in this site. While Malagasy forests are characterized by a mix of plant species with highly and loosely synchronized fruiting (Bollen and Donati, 2006), the dispersion of fruiting events within species was significantly clumped (seasonal) in Vatoharanana, but not in Talatakely. These results are of critical importance: *Eulemur rubriventer* are primarily fruit consumers (Overdorff, 1993ab, 1996ab; Tecot, 2007a) and the availability of fruit has a large impact upon behavioral and physiological energetic strategies (Tecot,

Chapter 3). Unpredictable availability of ripe fruit in the disturbed forest may have great implications for life history strategies in these groups.

Leaf flushing was drastically different between sites, with the nadir in Talatakely coincident with the zenith in Vatoharanana, and a study-long range of 40-80% presence in Talatakely versus 70 – 93% in Vatoharanana in any given month. Flowering was trimodal in each site (versus bimodal in 1988, Overdorff, 1992), and July was a peak flowering month in both sites. Less time was spent feeding on flowers in Talatakely compared with Vatoharanana by *Eulemur rubriventer* during peak flowering, and may be due to lower flower abundance in that site.

Phenological Seasons: Fruit

Fruiting was highly seasonal and the majority of tree species fruited synchronously, though many species fruited uniformly or randomly. Studies in other sites in Madagascar similarly found highly variable fruiting synchrony (Wright, 1999; Balko and Underwood, 2005; Bollen and Donati, 2006), as did studies in forests of other countries (Gautier-Hion *et al.,* 1981; van Schaik 1986; van Schaik *et al.* 1993). The lower number of flowering versus fruiting events observed in this study is unusual, and may have resulted from the monthly sampling schedule, as some flowers lead very short existences (S. Johnson, 2002).

The main peak in fruiting occurred in February (Vatoharanana; peaks were not discernible in Talatakely) and remained elevated through June (Figure 2.21). However, April though July or August is typically a lean period in Ranomafana, specifically Vatoharanana (Overdorff, 1991, 1992, 1993ab; Meyers and Wright, 1993; Hemingway, 1996, 1998; Balko, 1998; Overdorff and Wright, unpublished manuscript). In this site as well as in several other littoral (Bollen and Donati, 2006), low-altitude rainforest, and

mid-altitude rainforest sites in Madagascar (Vasey, 2000; see Bollen and Donati, 2006 and refs. within), October is a noted period of fruit abundance. Whether ripe fruit, unripe fruit, total fruit, or fruit exploited by *Eulemur rubriventer* was analyzed, October in this study (2003 and 2004) was a period of fruit scarcity (as was also reported by Balko (1998) and Balko and Underwood (2005) following a cyclone the prior March).

Balko and Underwood (2005) note that the steady rise in fruit availability from September through October is coincident with the *Varecia* birth season. This time of year is also coincident with the birth season of *Eulemur rubriventer*. If *all* food resources are considered, availability did steadily increase September through October (just prior to a decrease in October). However, this is a time of waning *fruit* abundance and one of the lowest periods of the year for fruit available on tree species consumed by *Eulemur rubriventer*. This can have important consequences for reproduction in several lemur species in this forest. However, while this period was consistently deficient in fruit in 2003 and 2004, differences in the number of births in these years (0% versus 100%, respectively) and the 100% survival rate of infants born at this time indicate that fruit availability at birth may not be critical. Alternatively, or additionally, food abundance *prior to* periods of food scarcity may be critical in sustaining individuals through the harshest seasons (Pereira *et al.,* 1999), and the abundance of fruit earlier in the year may facilitate storage of energy to be used around the time of birth.

A more important time of year may be late-lactation/early weaning (van Schaik and van Noordwijk, 1985; Wright, 1999), the most energetically expensive time for females (Jolly, 1984; Coelho, 1986; Bronson and Heideman, 1994), and which does occur in this species at the beginning of the increase in fruit availability (January). Balko and Underwood (2005) also reported fruit peaks in February and June, a finding which is

more consistent with this study and the assertion that these lemurs utilize a strategy of obligate reproduction, seen in highly seasonal environments whereby individuals time late-lactation and weaning with food abundance (Negus and Berger, 1972; Drent and Daan, 1980; May and Rubenstein, 1985; van Schaik and van Noordwijk, 1985; Wright, 1999). If phenological cycling is unpredictable, as it is in Talatakely, this strategy may not be successful. In fact, three out-of-season births occurred in these groups (while none occurred in Vatoharanana), all unsuccessful (deaths occurred within 3 months) (Tecot and Overdorff, 2005). Differences between studies at this site are likely due to the great inter-annual unpredictability in fruit availability documented by Overdorff and Wright (unpublished manuscript).

Phenological Seasons: New Leaves

Peaks in leaf flushing were mainly due to a few synchronous species. The most common time for peak flushing in both sites was February and troughs occurred in July (Talatakely) and August (Vatoharanana) (Figure 2.21). Other studies also found that February was the most common time of year for peak flushing (Overdorff and Wright, unpublished manuscript), and that new leaves were scarce in April, after the heavy rains of the cyclone season (Balko, 1998). While a steady decline in flushing occurred April through July in Talatakely, there was no indication of such rains affecting new leaf abundance in Vatoharanana.

Overall, new leaves comprise approximately 10% of *Eulemur rubriventer*'s diet, and *E. rubriventer* shift to a more fibrous, lower quality diet largely consisting of leaves and unripe fruit during the lean season (Overdorff, 1991, 1993a; Tecot, 2007a). Pereira *et al.,* (1999) suggest that new leaf feeding provides sustenance during the austral spring, a period when fruit is scarce and infants are born. However, flushing peaks did not occur

during the austral spring, and new leaf feeding did not occur more than 5% of the time in either site in the spring, and did not occur more than 10% of the time in any given month (Tecot, 2007a). Mature leaves appear to be more important in the diet of *E. rubriventer*. For instance, groups in Vatoharanana spent approximately 55% of their feeding time exploiting mature leaves in June, and those in Talatakely spent approximately 25% of their feeding time exploiting mature leaves in May (Tecot, 2007a). However, during the austral spring, mature leaf feeding did not occur greater than 5% of the time (Tecot, 2007a). Thus, these data do not support the assertion that leaves bolster the impact of austral spring fruit shortages in *Eulemur rubriventer* (*contra* Pereira *et al.,* 1999).

Interestingly, many species initiate breeding in response to cues received directly from eating vegetation such as grass and young Monocot shoots (see Negus and Berger, 1972; Berger *et al.,* 1981; Nelson *et al.,* 2002), and *Eulemur rubriventer* feeding data indicate a marked increase in mature leaf feeding prior to mating compared with all other times of the year (Tecot, 2007a). Although feeding upon new leaves did not increase, the age of mature leaves in evergreen forests may vary, and younger mature leaves are higher in nutrient content than older mature leaves (Ganzhorn *et al.,* 2003b). Thus, if newly mature leaves are being consumed, they may convey information about the availability of food in the future, and ultimately for reproduction. Phytochemical analyses of mature leaves consumed during the pre-breeding and breeding season compared with those consumed throughout the year would determine the importance of this item in providing short-term cues necessary to determine optimal strategies for energy allocation and reproduction (Wingfield, 2005).

Phenological Seasons: Flowers

Eulemur rubriventer may be important pollinators in Ranomafana, and although flowers are not a keystone resource for this species (Overdorff, 1992), they may provide essential nutrients during fruit scarcity, particularly the austral spring (September through November) (Pereira *et al.,* 1999). Flowers were abundant in each site when fruit was declining and low and new leaves were scarce. Flowering was largely synchronized within species (see above) and highly seasonal. There were three main periods of flower abundance throughout the study (December/January, July, and October/November) and results were highly variable across years and studies (*cf* Overdorff, 1992; Balko, 1998; S. Johnson, 2002; Overdorff and Wright, unpublished manuscript), as well as sites (Figure 2.21).

Flowering in October and November has also been noted to occur in both Ranomafana National Park and St. Luce (Overdorff, 1992; Bollen and Donati, 2005) when the weather is drier and irradiance is stronger (van Schaik *et al.,* 1993; Bollen and Donati, 2005). During this study, this period corresponded to decreasing fruit availability. However, the peak in October should not be considered a functional peak in flowering for *E. rubriventer*. In Overdorff's study which took place in 1988, this peak was actually minimal as was time spent flower feeding (Overdorff, 1992). During this study the peak in flowering was mainly due to *Tabernaemontana sp.* "vangindambo" (Apocynaceae), which was not consumed by *E. rubriventer.*

During this study, the peak flowering season occurred in December/January (in Vatoharanana), a period when high flowering has been previously documented for this forest (Overdorff, 1992). This was by far the greatest flowering period considering all species, as well as only consumed species, in terms of percent of trees and number of species flowering (see Table 2.11). This period was also coincident with peak flower

feeding (Tecot, this study) and the end of the fruit-scarce period (variable fruit abundance), suggesting that flowers may be important when infants begin to wean, rather than around the spring equinox during maximal scarcity and energy extraction from stores (Pereira *et al.,* 1999). Results from Overdorff's (1992) study also do not support a role for flowers as a critical resource during the austral spring equinox. Peak availability occurred November through February, which was not coincident with greatest fruit scarcity. However, peak flower feeding occurred in January (around weaning) and July/August (during increasing fruit availability).

These results suggest that flowering may not be a reliable resource during fruit scarcity, and not reliably available in particular months year to year (see also Overdorff, 1992). However, flowers may be reliably available at some point throughout the weaning process and contribute to energy storage necessary for later fruit shortages, thus helping species avoid stress, rather than cope with stress (*cf* Pereira *et al.,* 1999).

Synchrony of Food Seasons

Interestingly, in an extensive review of the literature Bollen and Donati (2005) report that all phenophases are synchronous in Malagasy rainforests. However, in Vatoharanana in this study leaves and fruits were abundant when flowers were scarce, and vice versa. November was the only time when the scarce seasons of all food types converged. The pattern is more difficult to decipher in Talatakely. While leaves occurred inversely with flowers, as in Vatoharanana during the first half of the study, leaves and flowers were abundant when fruit was scarce in the second half. Thus, animals in these forests may be able to compensate with other food sources during the lean season. Incongruities may be due to the broader (tree size) sampling regime

employed in this study, or inter-annual variability (Overdorff and Wright, unpublished manuscript).

Exploited Species

Establishing food availability seasons by phenological sampling in botanical plots yielded similar results to establishing seasons by sampling only known *Eulemur rubriventer* foods. This is a practical result since it is not always easy to determine food preferences on a taxonomic level prior to the desired establishment of botanical plots. While these results are only applicable to this species at these sites, it may facilitate future research on this species in Ranomafana. It has yet to be determined if this is true for fruit specialists in general or just *Eulemur rubriventer*. For a list of all observed *E. rubriventer* foods by site see Appendices 1 and 2.

A large majority of species exploited by *Eulemur rubriventer* were seasonal, approximately 13% were random, and approximately 4% were uniform. Looking specifically at consumed species and the particular phenophases for which each species was a food item, it appears that synchrony alone did not determine why certain species were chosen over others for food.

Unripe fruit has been proven to be a rarely consumed, yet important resource for *Eulemur rubriventer,* particularly in Talatakely. Phenological assessments indicated that no ripe fruit was present following cyclone Elita in March 2004. At this critical time just after weaning and just prior to the mating season, *Eulemur rubriventer* in Talatakely solely subsisted upon guava (*Psidium cattleianum*) (Tecot, this study). Other frugivores in this forest (*e.g., Eulemur fulvus rufus*) spend a substantial amount of time feeding upon unripe guava as well (Overdorff, personal communication), suggesting that this species is a good candidate for a fallback resource since it is available and exploited during

maximum fruit scarcity. Interestingly, fecal cortisol levels at this time are very low in the Talatakely population, despite the complete absence of ripe fruit available in the environment (Tecot, Chapter 4). In support of Durham's (2003) suggestion that guava may benefit these groups during the lean season, these results indicate that guava may fill a dietary void, providing sufficient nutrients and energy for this species to avoid energetic stress and a perceived food trough. Furthermore, guava fruits predictably year to year. This study found that overall *Eulemur rubriventer* in Talatakely exploit more unpredictable fruit resources than lemurs in Vatoharana, and a predictable resource in that site may be essential to their success.

Climate and Phenology

Lean periods often coincide with winter (Nelson *et al.,* 2002), and while this is typically viewed as a problem of negotiating high energetic demands with low energy availability in non-tropical species, tropical species are also affected by natural seasonal fluctuations in food availability and climate (van Schaik *et al.*, 1993). Thus it is important to understand the relationship between these factors when considering a primary consumer's energetic strategy.

Phenology and climate were correlated. Inter-site differences in the nature of this relationship were apparent, but the prediction that this relationship would be weaker in Talatakely, the disturbed site, was only partially supported. Further analyses separating alien and native tree species may help understand the impact of plant species tenure upon plant/climate relationships.

There was a great deal of variation between sites in the strength of the relationship between climate and phenological stage (Figure 2.21). This supports the assertion that climate is not always related to phenology in Ranomafana (Wright, 1999; Overdorff and

Wright, unpublished manuscript), and that other factors such as soil and canopy cover probably play significant roles (Sørg and Røhner, 1996; Grassi, 2001; B. Johnson, 2002; Bollen and Donati, 2005). For instance, hard rains in a more open landscape may affect the presence of fruits and inflourescences moreso than in a closed habitat by forcing them off trees and to the ground. This is supported by the weaker relationship between rainfall, fruits, and leaves in Talatakely. Rainfall may bring fruit in both sites, but more fruit may be sacrificed in Talatakely. Moreover, the relationship between leaf flushing and temperature was weaker in Talatakely. When Dataset 2 was analyzed, there was a significant correlation between fruiting and both rainfall and minimum temperature in Vatoharanana (as reported for Ranomafana by Atsalis, 1999aa and Kibale by Chapman *et al.,* 1999), but no significant correlations existed in Talatakely. This may indicate that rainfall and temperature are less reliable indicators/cues for *Eulemur rubriventer* food availability at this site. If fruiting phenology is not correlated with rainfall or temperature, and the confluence of climatic and phenological parameters is not predictable, energetic strategies in the disturbed site may be based upon short-term cues in the immediate environment rather than long-term cues regarding the availability of food in the future.

The overall relationship between climate and phenology was complex (Figure 2.21). Rainfall is often cited as the most influential factor in the timing of plant phenophase (Sørg and Røhner, 1996; Morellato *et al.* 2000), and inter-annually unpredictable rainfall patterns in Madagascar are suggested to influence lemur life histories via their impact on fruiting phenology (Dewar and Richard, 2007). Although recent analyses determined that this relationship is not a hard and fast rule (see van Schaik and Pfannes, 2005 and Bollen and Donati, 2006), rainfall and fruiting were

positively correlated in this study and positive relationships between these parameters have been found previously (Hemingway, 1996; Sørg and Røhner, 1996).

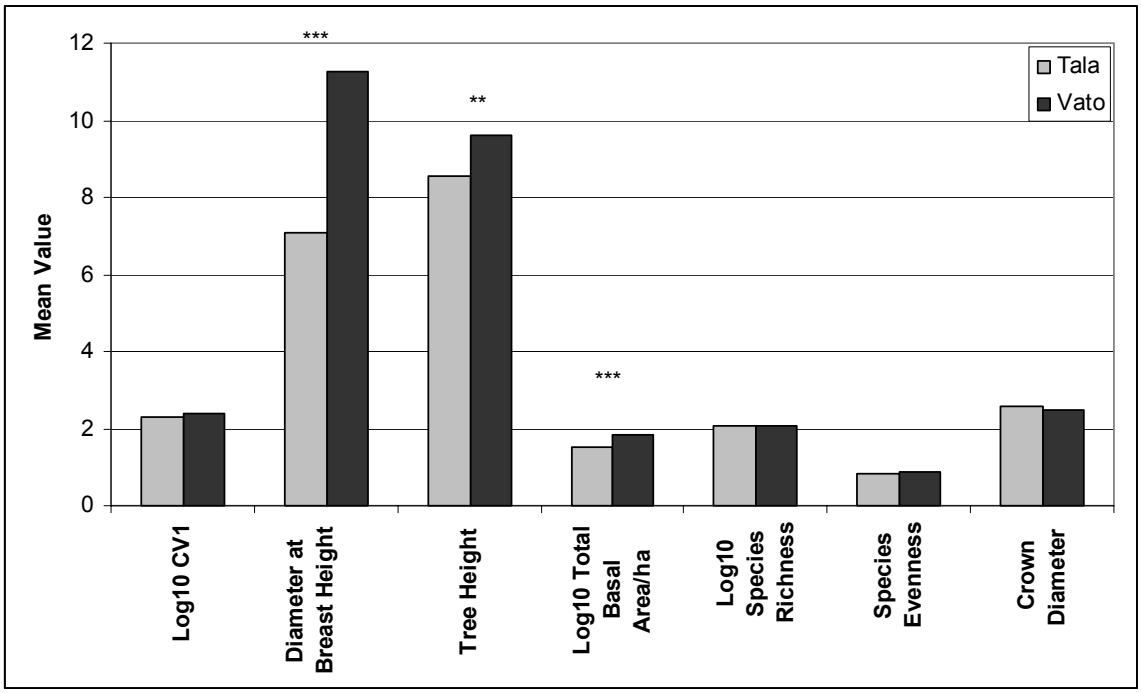
In general, fruit was lowest with low and increasing rain, and highest with high and declining rains. While fruiting occurred when maximum temperatures were low, fruiting (of all and exploited trees) also occurred when *minimum* temperatures were *high* in Vatoharanana, so no clear relationship was evident between fruiting and temperature.

Leaves flushed in both sites when the climate was warm and wet. A similar relationship between temperature and leaf flushing was found in St. Luce (Bollen and Donati, 2005). The same relationship between leaves and rainfall has been found for a variety of forest types (van Schaik *et al.,* 1993), and may be strongest in more seasonal habitats (van Schaik and Pfannes, 2005). In Madagascar, habitats in which a relationship between rainfall and leaf flushing was found range from the dry forests of Kirindy (Sørg and Røhner, 1996) to the littoral forests of St. Luce (Bollen and Donati, 2005), and the rain forests of Ranomafana (Hemingway, 1996, 1998).

Site differences in flowering precluded any determination of a general phenology-climate relationship for Ranomafana, though the positive relationship between rainfall and flowering in Vatoharanana found in this study has been reported previously for this site (Hemingway, 1996), and other seasonal primate habitats (van Schaik and Pfannes, 2005).

It should be noted that broad correlations are simplistic and should be viewed with caution. Any apparent disparity between phenological and climatological cycling may be due to either unsuccessful fruit setting or climatic events occurring up to one year prior to the study period. Johnson (2002) further considered climate parameters 11 months prior to phenological events (as per Chapman *et al.,* 1999), and found

relationships between temperature and leaf flushing and flowering, and rainfall and flowering, supporting the findings of this study. However, daylength, cloud cover, and irradiance were not investigated here, and as noted above, other studies indicate that they directly influence plant phenophase as well (van Schaik *et al.,* 1993; Wright and van Schaik 1994; Bollen and Donati, 2005).



[1]Crown volume data from Balko, 1998.

Figure 2.20. Features of the forest communities of Talatakely and Vatoharanana.

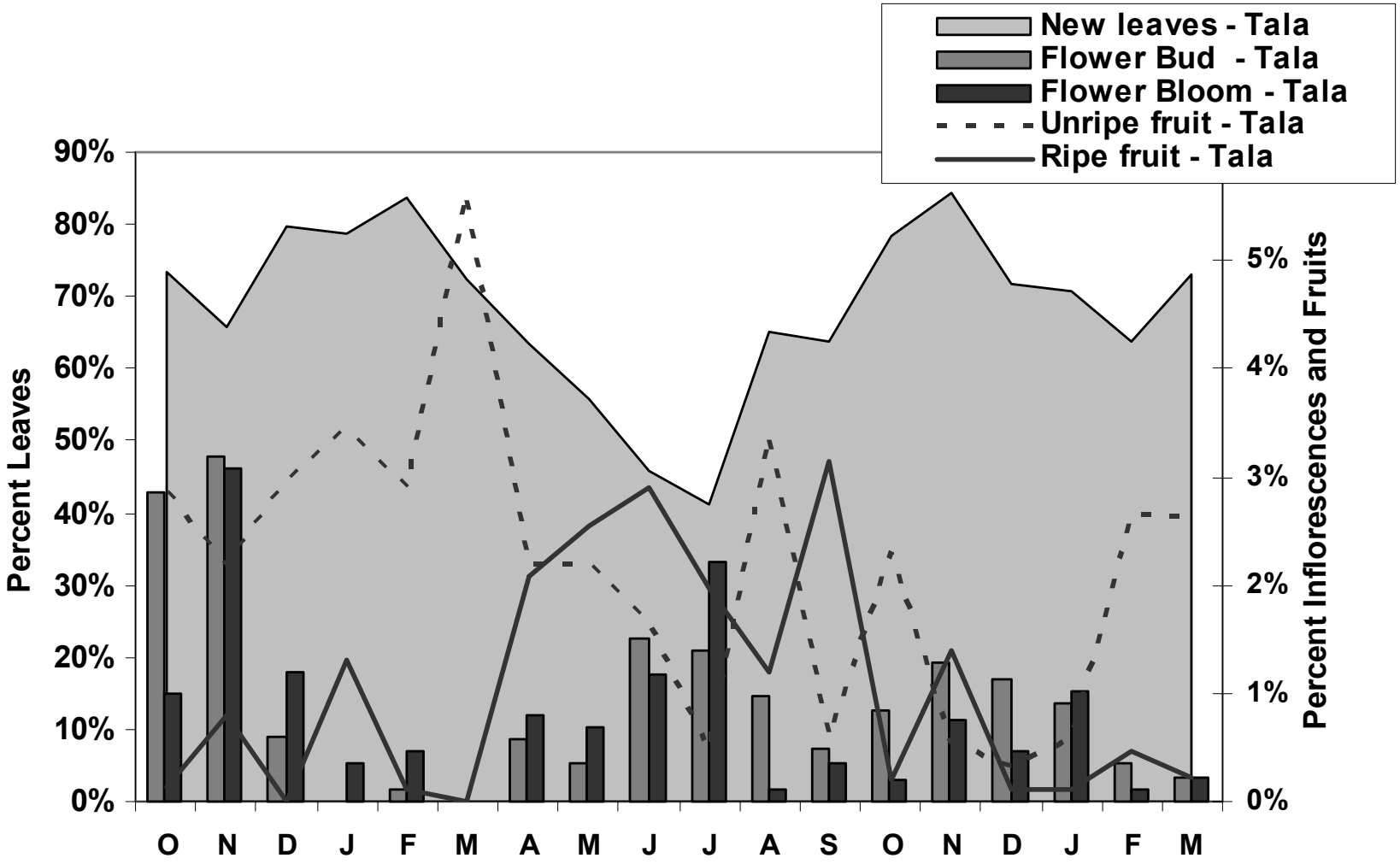
CONCLUSIONS

In this study forest quality, diversity, and productivity were higher in Vatoharanana, the undisturbed site. Phenological changes were seasonal with clearly delineated scarce and abundant seasons, yet seasonality was less predictable in Talatakely, the disturbed site, where lean seasons were prolonged and abundant seasons

were condensed. Seasonal changes in rainfall and temperature were apparent, with clearly delineated wet/warm, warm/dry, and cold/dry seasons. Phenology and climate were related, but this relationship was weaker in Talatakely, suggestive of the abundance of alien species with a shorter evolutionary history at this site.

These sites, Talatakely and Vatoharanana, remain different today in forest structure and composition, and it may be unreasonable to expect that they will ever be similar (Connell, 1978; Brown and Gurevitch, 2004). These sites should be considered functionally different when studying groups of a species occupying both sites. In particular, the quality, abundance, diversity, and predictability of resources which are available to groups of *Eulemur rubriventer* are highly variable from site to site. If this species relies upon food as an environmental cue for reproductive timing strategies (Wright, 1999; Tecot, Chapter 1), site differences may result in different reproductive schedules for groups a mere 6 km apart. Furthermore, small-scale disturbances such as selective extraction of resources may have great implications for the reproduction and survivorship of primary consumers.

(A) Talatakely



(B) Vatoharanana

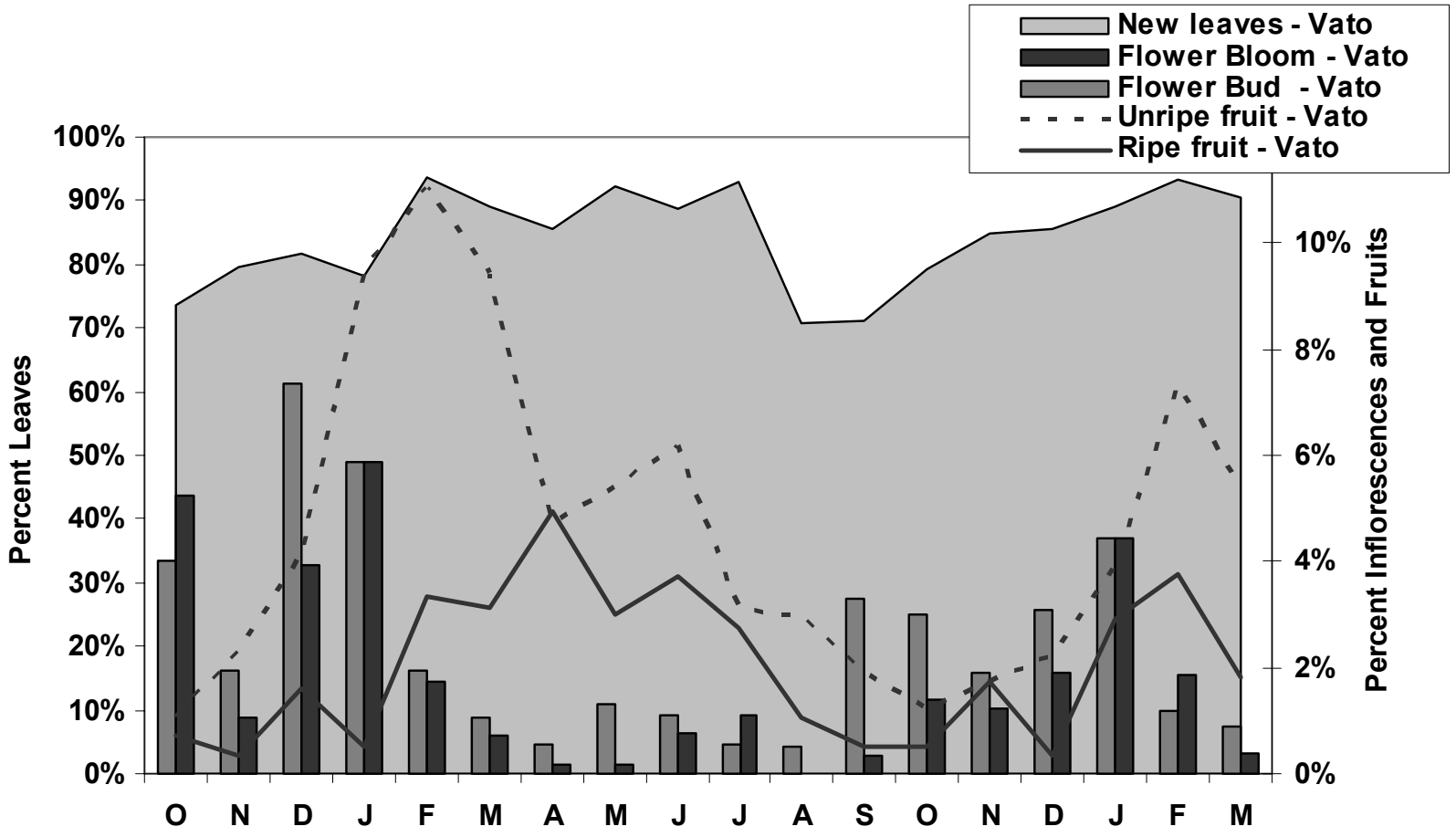


Figure 2.21. Phenological pattern of leaves, fruits, and inflorescences in (A) Talatakely and (B) Vatoharanana. New leaf abundance is represented by the area plot; fruits are represented by bars; flowers are represented by lines.

References

Arrigo-Nelson, S.J. 2006. *The Impact of Habitat Disturbance on the Feeding Ecology of the Milne-Edwards' Sifaka* (Propithecus edwardsi) *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Stony Brook: Stony Brook University, 181 p.

Atsalis, S. 1998. *Seasonal patterns in diet, distribution and reproduction of* Microcebus rufus *in the rain forest of Madagascar* [Doctoral Dissertation]. New York: City University of New York.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Balko, E.A. 1998. *A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by* Varecia variegata variegata *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Syracuse, NY: SUNY-CESF. 245 p.

Balko, E.A. and Underwood, H.B. 2005. Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*. 66(1):45-70.

Bawa, K.S. and Hadley, M. 1990. *Reproductive Ecology of Tropical Forest Plants*. Carnforth: Parthenon.

Begon, M., Harper, J.L., Townsend, C.R. 1990. *Ecology: Individuals, Populations and Communities, 2nd edition*. Brookline, MA: Blackwell Scientific.

Berenbaum, M.R. 2007. *Colony Collapse Disorder and Pollinator Decline*. Statement before the Subcommittee on Horticulture and Organic Agriculture, U.S. House of Representatives.

Berger, P.J., Negus, N.C., Sanders, E.H., Gardner, P.D. 1981. Chemical triggering of reproduction in *Microtus montanus*. *Science*. 214(4516):69-70.

Birkinshaw, C.R. and Colquhoun, I.C. 1998. Pollination of *Ravenala madagascariensis* and *Parkia madagascariensis* by *Eulemur macaco* in Madagascar. *Folia Primatologica*. 69(5):252-259.

Boinski, S. 1987. Habitat use by squirrel monkeys in a tropical lowland forest. *Folia Primatologica*. 49:151-167.

Bollen, A. and Donati, G. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*. 37(1):32-43.

Britt, A. 2000. Diet and feeding behaviour of the black-and-white ruffed lemur *(Varecia variegata variegata)* in the Betampona Reserve, eastern Madagascar. *Folia Primatologica*. 71(3):133-141.

Bronson, F.H. and Heideman, P.D. 1994. Seasonal regulation of reproduction in mammals. In: E. Knobil and J. D. Neil, editors. *The Physiology of Reproduction, 2nd ed*. New York: Raven Press.

Brown, K.A. and Gurevitch, J. 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences*. 101(16):6045-6049.

Brugiere, D., Gautier, J.P., Moungazi, A., Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest Gabon. *International Journal of Primatology*. 23(5):999-1024.

Cade, B.S. 1997. Comparison of tree basal area and canopy cover in habitat models: Subalpine forest. *The Journal of Wildlife Management*. 61(2):326-335.

Cant, J.G.H., Youlatos, D., Rose, M.D. 2001. Locomotor behavior of *Lagothrix lagtricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. *Journal of Human Evolution*. 41:141-166.

Carthew, S.M. and Goldingay, R.L. 1997. Non-flying mammals as pollinators. *Trends in Ecology and Evolution*. 12(3):104-108.

Cavigelli, S.A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*. 57(4):935-944.

Chapman, C. 1988. Patch use and patch depletion by the spider and howling monkeys of Santa-Rosa National Park, Costa Rica. *Behaviour.* 105:99-116.

Chapman, C.A. 1987. Flexible diets of three species of Costa Rican primates. *Folia Primatologica*. 49:90-105.

Chapman, C.A., Chapman, L.J., Wrangham, R., Hunt, K., Gebo, D., Gardner, L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica*. 24:527-531.

Chapman, C.A., Wrangham, R., Chapman, L.J. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*. 26:160-171.

Chapman, C.A. and Chapman, L.J. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*. 40:215-232.

Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.L., Saj, T.L., Ziegler, T.E. 2006. Do food availability, parasitism, and stress have synergistic effects on Red Colobus populations living in forest fragments? *American Journal of Physical Anthropology*. 131:525-534.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K., Zanne, A.E. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*. 15:189-211.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K., Zanne, A.E. 2000. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*. 15(02):189-211.

Charnov, E. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.

Chen, X. 2003. Assessing phenology at the biome level. In: M. D. Schwartz, editor. *Phenology: An Integrative Environmental Science*. Dordecht: Kluwer Academic. Pp. 285-300.

Chivers, D.J. 1991. Species differences in tolerance to environmental change. In: H.O. Box, editor. *Primate Responses to Environmental Change*. New York: Chapman and Hall. Pp. 5-37.

Coe, M.J. and Isaac, F.M. 1965. Pollination of the baobab *(Adansonia digitata* L.) by the lesser bush baby *(Galago crasicaudatus* E. Geoffroy). *East African Wildlife Journal*. 3(123-124).

Coelho, A.M. 1986. Time and energy budgets. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology*. New York: Alan R. Liss. Pp. 141–166.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a non-equilibrium state. *Science*. 199(4335):1302-1310.

Curtis, D.J. and Rasmussen, M.A. 2002. Cathemerality in lemurs. *Evolutionary Anthropology*. S1:83-86.

Curtis, D.J., Zaramody, A., Martin, R.D. 1999. Cathemerality in the mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology*. 47(4):279-298.

Daan, S. and Tinbergen, J.M. 1997. Adaptation to Life Histories. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach, Fourth Edition*. Oxford: Blackwell Science. Pp. 311-333.

Dagosto, M. and Yamashita, N. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. *Primates*. 39(4):459-472.

Dasilva, G.L. 1992. The western black-and-white colobus as a low-energy strategist: Activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology*. 61(1):79-91.

DeJong, T.M. 1975. A comparison of three diversity indices based on their components of richness and evenness. *Oikos*. 26(2):222-227.

Dew, J.L. and Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica*. 30(3):425-437.

Dewar, R.E. and Richard, A.F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences*. 104(34):13723-13727.

Di Fiore, A. and Suarez, S. 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition*. (Advance Online Publication):1-13.

Donque, G. 1972. The climatology of Madagascar. In: R. Battistini and G. Richard-Vindard, editors. *Biogeography and Ecology of Madagascar*. The Hague: W. Junk. Pp. 87-144.

Dorr, L.J. 2003. Identifying Malagasy trees. *Bioscience*. 53(7):678-680.

Drent, R.H. and Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea*. 68(1-4):225-252.

Dufils, J.-M. 2003. Remaining forest ecology. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 88-96.

DuPuy, D.J., Moat, J. 1995. A refined classification of the primary vegetation based on the underlying geology: Using GIS to map its distribution and to assess its conservation status. In: W.R. Laurenco, editor. *Biogeography of Madagascar*. Paris: Unesco. Pp. 205-218.

DuPuy, D.J. and Moat, J. 2003. Using geological substrate to identify and map primary vegetation Types in Madagascar and the implications for planning biodiversity conservation. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 51 - 67.

Durham, D.L. 2003. *Variation in responses to forest disturbance and the risk of local extinction: A comparative study of wild* Eulemurs *at Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Davis: University of California, Davis. 170 p.

Elsom, E. 2002. *A Preliminary Inventory of the* Platynini *(Coleoptera: Carabidae) of Ranomafana National Park* [Master's Thesis]. San Francisco: San Francisco State University.

Estrada, A. and Coates-Estrada, R. 1985. A preliminary study of resource overlap between howling monkeys (*Alouatta palliata*) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 9:27-37.

Estrada, A., Juan-Solano, S., Ortíz Martínez, T., Coates-Estrada, R. 1999. Feeding and general activity patterns of a howler monkey *(Alouatta palliata)* troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology*. 48(3):167-183.

Ferrari, S.F. and Strier, K.B. 1992. Exploitation of *Mabea fistulifera* nectar by marmosets *(Callithrix flaviceps)* and muriquis *(Brachyteles arachnoides)* in south-east Brazil. *Journal of Tropical Ecology*. 8:225-239.

Ganzhorn, J.U. 1995a. Cyclones over Madagascar: Fate or fortune? *Ambio*. 24:124-125.

Ganzhorn, J.U. 2003. Habitat description and phenology. In: J.M. Setchell, Curtis, D.J., editor. *Field and Laboratory Methods in Primatology: A Practical Guide*. Cambridge: Cambridge University Press. Pp. 40-56.

Ganzhorn, J.U. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia*. 91(4):540-547.

Ganzhorn, J.U., Fietz, J., Rakotovao, E., Schwab, D., Zinner, D. 1999a. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*. 13:794-804.

Ganzhorn, J.U. 1995b. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*. 76(7):2084-2096.

Ganzhorn, J.U., Malcomber, S., Andrianantoanina, O., Goodman, S.M. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica*. 29(3):331-343.

Ganzhorn, J.U., Goodman, S.M., Dehgan, A. 2003a. Effects of forest fragmentation on small mammals and lemurs. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1228-1234.

Ganzhorn, J.U., Klaus, S., Ortmann, S., Schmid, J. 2003b. Adaptations to seasonality: Some primate and nonprimate examples. *Primate Life Histories and Socioecology*. Chicago: University of Chicago Press. Pp. 132.

Garber, P.A. 1988. Foraging decisions during nectar feeding by tamarin monkeys *(Saguinus mystax* and *Saguinus fuscicollis,* Callitrichidae, Primates) in Amazonian Peru. *Biotropica*. 20:100-106.

Gautier-Hion, A., Gautier, J.P., Quiris, R. 1981. Forest structure and food availability as complementary factors influencing the habitat use by a troop of monkeys *(Cercopithecus cephus)*. *Revue d'ecologie*. 35:511-536.

Gautier-Hion, A. and Michaloud, G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*. 70(6):1826-1833.

Glander, K.E. 1981. Feeding patterns in mantled howling monkeys In: A. Kamil and T. Sargent, editors. *Foraging Behavior: Ecological and Psychological Approaches*. New York: Garland Press. Pp. 231-258.

Goldsmith, M.L. 1999. Ecological constraints on the foraging effort of western gorillas *(Gorilla gorilla gorilla)* at Bai Hokou, Central African Republic. *International Journal of Primatology*. 20(1):1-23.

Goldstein, S.J. and Richard, A.F. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *International Journal of Primatology*. 10(6):531-567.

Goodman, S.M. and Ganzhorn, J.U. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Review of Ecology*. 52:321-329.

Gorchav, D.L. 1990. Pattern, adaptation, and constraint in fruiting synchrony within vertebrate-dispersed woody plants. *Oikos*. 58(2):169-180.

Grassi, C. 1998. Forest composition and bamboo distribution: influences on the distribution of *Hapalemur* species. *American Journal of Physical Anthropology*.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Gross, T. 1991. Development and use of fecal steroid analyses in captive exotic mammals and birds; *Society for Theriogenology, Proceedings of Annual Meeting*: Pp. 66-74.

Gursky, S. 2000. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*. 21:477-495.

Harcourt, A. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: T Caro, editor. *Behavioral Ecology and Conservation Biology*. New York: Oxford University Press. Pp. 56-79.

Hemingway, C.A. 1995. *Feeding and Reproductive Strategies of* Propithecus diadema edwardsi [Doctoral Dissertation]. Durham: Duke University.

Hemingway, C.A. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edward's sifaka, *Propithecus diadema edwardsi,* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 17:637-657.

Hemingway, C.A. 1998. Selectivity and variability in the diet of Milne-Edwards' sifakas *(Propithecus diadema edwardsi)*: Implications for folivory and seed-eating. *International Journal of Primatology*. 19(2):355-377.

Hemingway, C.A. and Bynum, N. 2005. The influence of seasonality on primate diet and ranging. In: D.K. Brockman, van Schaik, C.P., editor. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 57-104.

Hemingway, C.A. and Overdorff, D.J. 1999a. Food for thought: Evaluating phenological methods as food availability estimates. *American Journal of Physical Anthropology*. S28:149.

Hladik, A. 1980. The dry forest of the west coast of Madagascar: Climate, phenology, and food available for Prosimians. In: P. Charles Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, A. Schilling and J.J. Petter, editors. *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*. New York: Academic Press. Pp. 3-40.

Hladik, C.M. 1979. Diet and ecology of prosimians. In: G.A. Doyle and R.D. Martin, editors. *The Study of Prosimian Behavior*. London: Academic Press. Pp. 307-358.

Hladik, C.M. and Charles-Dominique, P. 1974. The behaviour and ecology of the sportive lemur *(Lepilemur mustelinus)* in relation to its dietary peculiarities. In: G.A. Doyle, R.D. Martin and A.C. Walker, editors. *Prosimian Biology*. London: Duckworth. Pp. 23-37.

Hubbell, S.P. and Foster, R.B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: S.L. Sutton, T.C Whitmore and A.C. Chadwick, editors. *Tropical Rain Forest: Ecology and Management* Oxford: Blackwell Scientific Publications. Pp. 25-41.

Irwin, M.T. 2006. *Ecological Impacts of Forest Fragmentation on Diademed Sifakas* (Propithecus diadema) *at Tsinjoarivo, eastern Madagascar: Implications for Conservation in Fragmented Landscapes* [PhD Dissertation]. Stony Brook, New York: Stony Brook University. 410 p.

Irwin, M.T. 2007. Living in forest fragments reduces group cohesion in diademed sifakas *(Propithecus diadema)* in eastern Madagascar by reducing food patch size. *American Journal of Primatology*. 69(4):434-447.

Janson, C. and Verdolin, J. 2005. Seasonality of primate births in relation to climate. In: D.K. Brockman, C.P. van Schaik and M.A. van Noordwijk, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 307-350.

Janson, C.H., Terborgh, J., Emmons, L.H. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica*. 14(1-6).

Johns, A.D. and Skorupa, J.P. 1987. Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*. 8(2):157-191.

Johnson, B.K. 2002. *Soil characterization and reconnaissance survey of the Ranomafana National Park area, southeastern Madagascar* [Doctoral Dissertation]. Raleigh, NC: North Carolina State University.

Johnson, R. 2007. *CRS Report for Congress: Recent Honey Bee Colony Declines.* Science Congressional Research Division. Resources and Industry Division. 13 p.

Johnson, S.E. 2002. *Ecology and Speciation in Brown Lemurs: White-collared Lemurs* (Eulemur albocollaris) *and Hybrids* (Eulemur albocollaris *X* Eulemur fulvus rufus) *in Southeastern Madagascar* [Doctoral Dissertation]. Austin: University of Texas at Austin. 288 p.

Jones, J.P.G., Andriahajaina, F.B., Hockley, N.J., Balmford, A., Ravoahangimalala, O.R. 2005. A multidisciplinary approach to assessing the sustainability of freshwater crayfish harvesting in Madagascar. *Conservation Biology*. 19(6):1863-1871.

Jury, M.R. 2003. The climate of Madagascar. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 75-87.

Kery, M. and Schmid, H. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology*. 43(1):101-110.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems & Environment*. 74(1-3):373-393.

Knott, C.D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*. 19:1061-1079.

Kowalewski, M.M. and Zunino, G.E. 1999. Impact of deforestation on a population of *Alouatta caraya* in northern Argentina. *Folia Primatologica*. 70(3):163-166.

Krebs, C.J. 1999. *Ecological Methodology*. Addison Wesley Longman, editor. Menlo Park, CA.

Kress, W.J., Schatz, G.E., Andrianifahanana, M., Morland, H.S. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: Evidence for an archaic coevolutionary system? *American Journal of Botany*. 81(5):542-551.

Leigh, E.G., Jr. 1999. *Tropical Forest Ecology: a View from Barro Colorado Island*. New York: Oxford University Press.

Leighton, M. and Leighton, D.R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick, editors. *Tropical Rain Forest: Ecology and Management*. Oxford: Blackwell. Pp. 181-196.

Lewis, R.J. and Kappeler, P.M. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*. 67(3):347-364.

Magurran, A.E. and Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*. 422(6933):714-716.

Marsh, C.W., Johns, A.D., Ayres, J.M. 1987. Effects of habitat disturbance on rain forest primates. In: C.W. Marsh and R.A. Mittermeier, editors. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 83-107.

Martin, R.D. 1972. A preliminary field-study of the Lesser Mouse Lemur *(Microcebus murinus* J. F. Miller 1977). In: P. Charles Dominique and R.D. Martin, editors. *Behaviour and Ecology of Nocturnal Prosimians*. Berlin: Paul Parey. Pp. 43-89.

May, R.M. and Rubenstein, D.I. 1985. Reproductive strategies. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals: Reproductive Fitness, Book 4*. New York: Cambridge University Press. Pp. 1-23.

Meyers, D.M. and Wright, P.C. 1993. Resource tracking: Food availability and *Propithecus* seasonal production. In: P.M. Kappler and Ganzhorn J.U., editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 179-192.

Miller, L.E. 2002. *Eat or be Eaten: Predator Sensitive Foraging among Primates*. New York: Cambridge University Press.

Miller, M.W., Hobbs, N.T., Sousa, M.C. 1991. Detecting stress responses in Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*): Reliability of cortisol concentrations in urine and feces. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 69(1):15-24.

Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Washington, DC: Smithsonian Institution Press. Pp. 273-289.

Monfort, S.L., Wasser, S.K., Mashburn, K.L., Burke, M., Brewer, B.A., Creel, S.R. 1997. Steroid metabolism and validation of noninvasive endocrine monitoring in the African wild dog *(Lycaon pictus)*. *Zoo Biology*. 16(6):533-548.

Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., Zipparro, V.B. 2000. Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*. 32(4b):811-823.

Morland, H.S. 1991. Preliminary report on the social organization of ruffed lemurs *(Varecia variegata variegata)* in a northeast Madagascar rainforest. *Folia Primatologica*. 56:157-161.

Morland, H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 193-203.

Negus, N.C. and Berger, P.J. 1972. Environmental factors and reproductive processes in mammalian populations. In: J.T. Velardo and B.A. Kasprow, editors. *Biology of Reproduction: Basic and Clinical Studies*; *Third Pan American Congress on Anatomy*, New Orleans. Pan American Association of Anatomy: Pp. 89-98.

Nelson, R.J., Demas, G.E., Klein, S.L., Kriegsfeld, L.J. 2002. *Seasonal Patterns of Stress, Immune Function, and Disease*. New York: Cambridge University Press.

Nilsson, L.A., Rabakonandrianina, E., Pettersson, B., Gruenmeier, R. 1993. Lemur pollination in the Malagasy rainforest liana *Strongylodon craveniae* (Leguminosae). *Evolutionary Trends in Plants*. 7(2):49-56.

Oates, J. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*. 21:1-9.

Oates, J.F. 1977. The guereza and its food. In: T.H. Clutton-Brock, editor. *Primate Ecology*. London: Academic Press. Pp. 276-319.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L., Mole, S. 1990. Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology*. 71(1):328-343.

Onderdonk, D.A. and Chapman, C.A. 2000. Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology*. 21(4):587-611.

Overdorff, D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D.J. 1991. *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral dissertation]. *Durham: Duke University. 313 p.* Durham: Duke University. 313 p.

Overdorff, D.J. 1992. Differential patterns in flower feeding by *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. *American Journal of Primatology*. 28:191-203.

Overdorff, D.J. 1993a. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. *International Journal of Primatology*. 14(5):721-753.

Overdorff, D.J. 1993b. Ecological and reproductive correlates to range use in red-bellied lemurs *(Eulemur rubriventer)* and rufous lemurs *(Eulemur fulvus rufus)*. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 167-178.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40(4):327-342.

Overdorff, D.J. 1996b. Ecological correlates to social structure in two Lemur species in Madagascar. *American Journal of Physical Anthropology*. 100(4):487-506.

Overdorff, D.J. and Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Overdorff, D.J., and Tecot, S. R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 235-245.

Overdorff, D.J., Merenlender, A.M., Talata, P., Telo, A., Forward, A.Z. 1999. Life history of *Eulemur fulvus rufus* from 1988-1997: Implications for ecological stress in southeastern Madagascar. *American Journal of Physical Anthropology.* 108:295-310.

Passamini, M. 1998. Activity budget of Geoffroy's Marmoset *(Callithrix geoffroyi)* in an Atlantic forest in Southeastern Brazil. *American Journal of Primatology*. 46:333-340.

Pereira, M.E., Russ, A.S., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Publishers.

Peters, J. 1999. Understanding Conflicts between People and Parks at Ranomafana, Madagascar. *Agriculture and Human Values*. 16(1):65-74.

Petter, J.J. 1978. Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variations in food production. In: D.J. Chivers and J. Herbert, editors. *Recent Advances in Primatology, Vol. 1*. New York, NY: Academic Press. Pp. 211-223.

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A., Vasquez, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Association of Science*. 91(7):2805-2809.

Pianka, E. 1994. *Evolutionary Ecology, 5th edition*. New York, NY: Harper Collins.

Prance, G.T. 1980. A note on the probable pollination of *Combretum* by *Cebus* monkeys. *Biotropica*. 12:239.

Purvis, A. and Hector, A. 2000. Getting the measure of biodiversity. *Nature*. 405(6783):212-219.

Raju, A.J.S. and Rao, S.P. 2006. Pollination by bees and passerine birds and seed dispersal by monkeys in the white teak *Gmelina arborea* Roxb., a commercially important timber tree species in the Eastern Ghats. *Current Science*. 90(2):232-236.

Rasamimanana, H.R. and Rafidinarivo, E. 1993. Feeding behavior of *Lemur catta* females in relation to their physiological state. *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 123-133.

Ratsimbazafy, J. 2002. *On the brink of extinction and the process of recovery: responses of black-and-white ruffed lemurs* (Varecia variegata variegata) *to disturbance in Manombo Forest, Madagascar* [Doctoral Dissertation]. Stony Brook, NY: State University New York at Stony Brook.

Ratsimbazafy, J. 2006. Diet composition, foraging, and feeding behavior in relation to habitat disturbance: Implications for the adaptability of ruffed lemurs *(Varecia v. editorum)* in Manombo Forest, Madagascar. In: L. Gould and M.L. Sauther, editors. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 403-422.

Remaharitra, T. 2006. The effects of anthropogenic disturbances on the structure and composition of rain forest vegetation. *Tropical Resources Bulletin*. 25:32-37.

Rennolls, K. and Laumonier, Y. 2000. Species diversity structure analysis at two sites in the tropical rain forest of Sumatra. *Journal of Tropical Ecology*. 16:253-270.

Richard, A.F. 1978. Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi:* Lemuriformes. In: G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Washington, D.C.: Smithsonian Institute Press. Pp. 519-533.

Richard, A.F., Sussman, R. W. 1987. Framework for primate conservation in Madagascar. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 329-341.

Riley, E.P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alternation. *International Journal of Primatology*. 28(1):107-133.

Risler, L., Wasser, S.K., Sackett, G.P. 1987. Measurement of excreted steroids in *Macaca nemestrina*. *American Journal of Primatology*. 12(1):91-100.

Sagar, R. and Singh, J.S. 2006. Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: implications for conservation. *Environmental Conservation*. 33(3):256-262.

Sauther, M.L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ringtailed lemur conservation. *Folia Primatologica*. 69:309-320.

Schatz, G.E. 2001. *Generic Tree Flora of Madagascar*. Kew: Missouri Botanical Gardens and Royal Botanic Garden.

Schmid, J., Kappeler, P.M. 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur *(Microcebus murinus)*. *Behavioural Ecology and Sociobiology*. 43:125-132.

Shannon, C.E. and Weaver, W. 1963. *Mathematical Theory of Communication*. Chicago: University of Illinois Press.

Simpson, E.H. 1949. Measurement of diversity. *Nature*. 163:688.

Singh, L. and Singh, J.S. 1991. Species structure, dry matter dynamics and carbon flux of a dry tropical forest in India. *Annals of Botany*. 68:263-273.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*. New York: W. H. Freeman.

Sørg, J.-P. and Røhner, U. 1996. Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. *Primate Report*. 46(1):57-80.

Southwood, T.R.E. 1978. *Ecological methods: with particular reference to the study of insect populations*. London: Chapman & Hall.

Spellerberg, I.F. and Fedor, P.J. 2003. A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. *Global Ecology and Biogeography*. 12(3):177-179.

Stavisky, R.C., Brandenberger, D., Hook, M., Russell, E., Kaplan, J., Whitten, P. 2001b. The effect of menstrual cycle phase on cortisol excretion on female cynomolgus monkeys *(Macaca fascicularis)*. *American Journal of Primatology*. 54(S1):39-40.

Struhsaker, T.T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Gainseville: University Press of Florida.

Sussman, R.W. and Raven, P.H. 1978. Pollination by lemurs and marsupials: an archaic evolutionary system. *Science*. 200:731-736.

Swarup, A. 2007. Red Cross -- Red Crescent respond to cyclones in Madagascar. International Federation of Red Cross and Red Crescent Societies (IFRC)--Switzerland.

Tan, C.L. 2000. *Behavior and ecology of three sympatric bamboo lemur species (genus* Hapalemur*) in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. New York: State University of New York at Stony Brook.

Tecot, S. 2007a. Seasonality, phenology, and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. S44:230.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Terborgh, J. 1986a. Community aspects of frugivory in tropical forests. In: A. Estrada and T.H. Fleming, editors. *Frugivores and Seed Dispersal*. Dordrecht: Dr. W. Junk Publishers. Pp. 372-384.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton, N.J.: Princeton University Press.

Terborgh, J. 1986b. Keystone plant resources in the tropical forest. In: M.E. Soulé, editor. *Conservation Biology, the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc. Pp. 330–344.

Torres de Assumpção, C. 1981. *Cebus apella* and *Brachyteles arachnoides* (Cebidae) as potential pollinators of *Mabea fistulifera* (Euphorbiaceae). *Journal of Mammalogy*. 62:386-388.

Traveset, A. 1999. The importance of mutualisms for biodiversity conservation in insular ecosystems. *Revista Chilena de Historia Natural*. 72(4):527-538.

Tsuji, Y., Fujita, S., Sugiura, H., Saito, C., Takatsuki, S. 2006. Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. *American Journal of Primatology*. 68:1068-1080.

Turk, D. 1995. *A Guide to Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Turk, D. 1997. *A Guide to Trees of Eastern Madagascar and Ranomafana National Park*. Missouri Botanical Garden, St. Louis.

Turner, I.M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology*. 33(2):200-209.

UNDP. 2006. *World Development Report*. Oxford: United Nations Development Programme.

van Schaik, C., and van Noordwijk, MA. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques *(Macaca fascicularis)*. *Journal of Zoology*. 206:533-549.

van Schaik, C.P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology*. 2:327-347.

van Schaik, C.P. and Pfannes, K.R. 2005. Tropical climates and phenology: a primate perspective. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 23-51.

van Schaik, C.P., Terborgh, J., Wright, S.J. 1994. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*. 24:353-377.

van Schaik, C.P., Terborgh, J.W., Wright, S.J. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*. 24:353-377.

Vasey, N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology*. 112(3):411-431.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs *(Varecia rubra)* on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. *American Journal of Primatology*. 66(4):393-394.

White, F., Overdorff, D.J., Balko, E., Wright, P.C. 1995. Distribution of ruffed lemurs *(Varecia variegata)* in Ranomafana National Park, Madagascar. *Folia Primatologica*. 64:124-131.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*. 21:213-251.

Whitten, P. 2000. Evolutionary endocrinology of the cercopithecoids. In: P.F. Whitehead and C.J. Jolly, editors. *Old World Monkeys*. Cambridge: Cambridge University Press. Pp. 269-297.

Whitten, P.L., Brockman, D.K., Stavisky, R.C. 1998a. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*. Pp. 1-23.

Whitten, P.L., Stavisky, R., Aureli, F., Russell, E. 1998b. Response of fecal cortisol to stress in captive chimpanzees *(Pan troglodytes)*. *American Journal of Primatology*. 44(1):57-69.

Wikelski, M., Hau, M., Wingfield, J.C. 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology*. 81(9):2458-2472.

Williamson, M. and Gaston, K.J. 2005. The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. *Journal of Animal Ecology*. 74(3):409-422.

Wingfield, J.C. 2005. Flexibility in annual cycles of birds: implications for endocrine control mechanisms. Journal of Ornithology. V146(4):291-304.

Wright, P.C. 1992. Primate ecology, rainforest conservation and economic development: Building a national park in Madagascar. *Evolutionary Anthropology*. 1:25-33.

Wright, P.C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 16(5):835-854.

Wright, P.C. 1997. The future of biodiversity in Madagascar: A view from Ranomafana National Park. In: S. G. Goodman and B. D. Patterson, editor. *Natural Change and Human Impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press. Pp. 381-405.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology. 42:31-72.

Wright, P.C. 2006. Considering Climate Change Effects in Lemur Ecology and Conservation. In: L. Gould and M.L. Sauther, editor. Lemurs: Ecology and Adaptation. New York: Springer. Pp. 385-401.

Wright, P.C. and Andriamihaja, B. 2002. Making a Rain Forest National Park Work in Madagascar: Ranomafana National Park and Its Long-term Research Commitment. In: J. Terborgh, C. van Schaik, L. Davenport and M. Rao, editors. Making Parks Work: Strategies for Preserving Tropical Nature. Washington: Island Press. Pp. 112-136.

Wright, P.C. and Martin, L.B. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 45-60.

Wright, P.C. and Razafindratsita, T., Pochron, S.T., Jernvall, J. 2005. The key to frugivory in Madagascar. In: J.L. Dew and J.P. Boubli, editors. *Tropical Fruits and Frugivores: The Search for Strong Interactors.* New York: Kluwer Academic/Plenum. Pp. 118-128.

Wright, S.J. and van Schaik, C.P. 1994. Light and the phenology of tropical trees. *American Naturalist*. 143:192-199.

Chapter 3: *Eulemur rubriventer* Energetics: The Influences of Climate, Resources, and Habitat on Time Budgets

INTRODUCTION

The study of animal time budgets is essential to better understand how species maximize energy intake and storage in order to survive and reproduce in an ever changing environment (Aschoff, 1964; Nielsen, 1983; Halle and Stenseth, 2000). Predation risk, reproductive condition, and competition all change with seasonal changes in day length, climate, and resources. On a proximate level, these changes impose moving targets for energetic homeostasis, and animals must make adjustments to mitigate the stress associated with these changes. Ultimately, the way that a species distributes its energy may impact its life history strategy and reproductive success.

Biological energy distribution is energy contained in food and the transfer of this energy to an animal (Coelho, 1986). The efficiency of this process in maintaining enough energy to function and reproduce is astounding given the complexity of the system. Coelho (1986) describes a model of the process whereby gross energy intake of food is converted into net energy for an animal. This model illustrates an intricately balanced system composed of metabolized, maintenance, and production energy. Energy distribution consists of gross energy (energy intake of food minus defecated energy), which is then used as metabolized energy (fuel) or excreted as urinary energy. Metabolized energy is used for maintenance or production, and released as heat energy (energy used to warm or cool an animal below or above the thermoneutral zone, respectively). Maintenance energy consists of basal metabolism, activity expenditure,

and the heat increment necessary to keep an animal in a thermoneutral state. Production energy consists of metabolic energy required for growth, development, energy storage, and reproduction. Thus, the food available to animals initiates a cascade of energy partitioning resulting in certain metabolic rates and behavior budgets.

Changes in activity to accommodate these different changing energetic needs can vary greatly among animals, even closely related species. The ways in which species vary their daily and seasonal time budgets can provide a more detailed assessment of energy strategies than measures such as metabolic rate due to the more plastic nature of behavior (Coelho, 1986; Vasey, 2005). Several species are able to adjust time spent feeding, resting, and traveling in an energetic (and risk) trade-off (Cuthill and Houston, 1997; Nash, 1998; Halle and Stenseth, 2000). Optimal Foraging Theory predicts that feeding and traveling change relative to one another. To maximize energy, animals may spend more time feeding and traveling to find quality food from diverse resources, or more time feeding on great amounts of low quality food; to minimize energy expenditure and time, animals may spend more time resting by spending less time feeding and/or traveling, settling for foods nearby when rare, high quality resources do not exist (Schoener, 1971; Cuthill and Houston, 1997). These patterns are then compounded by factors such as the quality and digestibility of food available, climate, and reproductive condition. Investigating seasonal fluctuations in the amount of time devoted to feeding, traveling, and resting behaviors informs on how species meet myriad challenges, including changing climate and food availability, since they are related to energy intake, conservation, and expenditure. Furthermore, determining the manner of behavioral flexibility employed by species in response to seasonal changes can indicate how they

might respond to natural or anthropogenic habitat alterations, an increasingly relevant topic in wildlife studies.

Climate

Changes in climate are highly likely to influence mammalian time budgets because of the climate's influence on thermoregulation and plant phenophase. Several studies have investigated time budget differences between warm and cool seasons and wet and dry seasons (e.g., see Nash 1998 for review). Such seasonal changes not only alter the thermal environment; rainfall, temperature, and a host of other interrelated factors (e.g., soil, fire, and topography) also influence the type and amount of nutrients available in a given environment ('chemical energy', Coelho, 1986; Ricklefs and Miller, 2000). Plant production corresponds to nutrient availability overall (determining what plant species are present) and seasonally (determining phenophase), and therefore climate can have a strong relationship with food availability which will in turn affect an organism's activity.

Species may respond to temperature changes by increasing or decreasing activity, depending upon the amount of heat production necessary to perform the activity. During experimental studies, mouse energy expenditure decreased with higher ambient temperatures, and energy expenditure (feeding activity) increased with lower ambient temperatures (Vaanholt *et al.*, 2007). Nevertheless, although lower temperatures prompted increased feeding activity, reduced locomotor (speed, distance, duration) activity occurred as well (Vaanholt *et al.*, 2007), indicating a trade-off between heat production (through activity) and heat conservation (through reduced activity).

Though largely restricted to the tropics, primates may be particularly influenced by climate changes, using either energy accumulating or time and energy minimizing strategies. As with mice, primate thermoregulatory hypotheses may predict decreased activity (or increased nocturnal activity) with *high* ambient temperatures in order to stay *cool* and avoid heat stress (Pollack, 1979; Engqvist and Richard, 1991; Richard and Dewar, 1991; Curtis *et al.*, 1999; Estrada *et al.,* 1999; Pereira *et al.*, 1999; Vaanholt *et al.*, 2007), and increased activity with *low* ambient temperatures to stay *warm* and avoid cold stress (Nash, 1998; Vaanholt *et al.*, 2007). Responses to rainfall may also be related to thermoregulation, with reduced activity during the wet season to spend more time huddling, enabling animals to use body heat to stay warm, and reducing heat energy expenditure. For instance, though mountain gorilla time budgets (feeding, resting, and moving) did not differ significantly between rainfall seasons, animals became inactive at the commencement of heavy rains, and continued until rains subsided unless they were prolonged throughout the day (Watts, 1988). However, the relationship between climate and time budget observed in primates is also equivocal, whereby feeding, resting, and traveling may vary in unpredictable ways. For instance, macaques *(Macaca fuscata)* decreased both feeding and traveling time during winter when temperatures were *low* (Hanya, 2004). Often such differences depend upon a species' diet and the availability of food.

Habitats with less seasonal climates contain more constant and diverse resources than more seasonal habitats (e.g., seasonal rain forest, dry forest) (Stoner, 1996), where plant production tracks climate seasonality. In fact, in a meta-analysis of seasonal phenology in tropical and woodland primate habitats, van Schaik and Pfannes (2005)

found that flushing and flowering increase with rainfall seasonality. Contrary to expectations, fruiting was not related to rainfall although they suggest that this relationship may be present in fruit with high water content (van Schaik and Pfannes, 2005). Such a relationship between particular food items and climate may explain some of the variability in activity adjustments between species with different diets in response to climate changes. For instance, in the seasonal northeastern rain forests of Madagascar, frugivorous red ruffed lemur (*Varecia rubra*) time budgets were directed towards accumulating energy (more feeding and resting, less traveling) during the hot/dry season when fruit was becoming abundant (Vasey, 2005). In contrast, folivorous species may focus more upon minimizing time and energy than accumulating energy (Neville *et al.*, 1988). During the dry season folivorous Colobus monkeys *(Colobus polykomos)* spent less time feeding and more time resting (Dasilva, 1992). This may be typical in folivorous species, as feeding on less digestible foods during the dry season may require longer digestion time (Powzyk, 1997), and a sacrifice of time spent feeding and traveling (Dasilva, 1992; Silver and Marsh, 2003). Similarly, within-species variation may occur where groups live in habitats with variable seasonality. While Stoner (1996) found no effect of time of year on mantled howler monkey time budgets, her study was conducted in a forest where there was no pronounced dry season. In sites where rainfall was more seasonal, howler monkey time budgets shifted between rainfall seasons, and Stoner (1996) relates these different responses to rainfall seasons to the variable plant production between sites.

Several studies of wild mammals (see Curtis and Rasmussen, 2006) have reported shifts in *daily* activity rhythm (the distribution of activities throughout the day) either to

stay warm or cool as ambient temperatures fluctuate, even in the tropics where daily temperature fluctuations are minimal (*e.g.,* Curtis *et al.*, 1999; Vasey, 2005; reviewed in Curtis and Rasmussen, 2002). The way in which animals reconcile these changing energetic demands may vary. For instance, baboons change the scheduling of activities throughout the day in response to heat, resting more as temperatures (and day lengths) increase (Hill, 2005, 2006), a similar strategy to those species who become less active during the warm season (*e.g.,* howler monkeys, Estrada *et al.,* 1999). However, cathemeral species such as the collared brown lemur (*Eulemur fulvus collaris*) and the rufous lemur (*Eulemur fulvus rufus*), which show more flexibility in the distribution of activity across the 24-hour period of a day (see below), may shift their peak times of activity to avoid cold stress. Erkert and Cramer (2006) suggest that cathemeral species may have nocturnal circadian rhythms. Heightened activity at night may be necessary during the cool season because lowest temperatures occur at night, require a greater heat increment, and pose the greatest risk; heightened activity during the day may be a *release* from nighttime activity (Erkert and Cramer, 2006; van Schaik and Kappeler, 1996). Greater nighttime activity during the cool season has been observed in several *Eulemur* species (Overdorff and Rasmussen, 1995; Curtis *et al.*, 1999; Donati *et al.*, 1999; Rasmussen, 1999; Kappeler and Erkert, 2003; Tarnaud, 2006), and cathemeral species may spend more time active during the day when nighttime temperatures are warmer (Donati and Borgognini-Tarli, 2006; Kappeler and Erkert, 2003). Results are variable however, and some species appear to respond to daytime temperatures. For instance, during the warm season increased nighttime activity has also been observed in *Eulemur* (Tattersalll, 1976), presumably to stay cooler during the day.

Primates therefore appear to be quite flexible, able to solve the energetic challenges posed by rainfall and temperature using a diverse array of behavioral modifications (see also Harcourt, 1991, Morland, 1993, Bicca-Marques and Calegaro-Marques, 1998, Nash, 1998, Wright, 1999, Pochron, 2000, Vasey, 2005, and Bearder *et al.*, 2006 for discussions of sun seeking and huddling behaviors; see Pochron, 2000 and Hill, 2006 for discussions of sun avoidance behaviors). Hill (2005) suggests that thermoregulatory responses may, however, be constrained by resource abundance and seasonality.

Resource Abundance and Seasonality

Although much has been written about seasonal changes in diet and activity, some animals may not adjust time budgets between food availability seasons. For instance, Ebensperger and Hurtado (2005) found that degus *(Octodon degus)* spent the same amount of time foraging during lean and abundant seasons. Although these results appear to suggest no constraint of food scarcity on these rodents, or conversely low energetic efficiency (Durham, 2003), the authors suggest that during the abundant season animals continued to feed for long periods of time to acquire sufficient energy for reproduction, thus canceling out any perceived adjustment (Ebensperger and Hurtado, 2005). Among primates, red ruffed lemur (*Varecia rubra*) females also did not shift the amount of time devoted to feeding between scarce and abundant resource seasons (Vasey, 2005). More commonly, however, animals will adjust time budgets to mitigate the stress of decreased resources.

Animals occupying different niches have the potential to differ in how they respond to seasonal changes that affect their ability to accumulate and/or conserve energy. The distribution, phenophase, productivity, and availability of resources are dynamic factors that can cause a variety of species to modify their diets in time and space (*e.g.,* Richard, 1978, Lewis and Kappeler, 2005, Norscia *et al.,* 2006 [*Propithecus*]; Glander, 1981 [*Alouatta*]; Boinski, 1987 [*Saimiri*]; Dasilva, 1992 [*Colobus*]; Overdorff, 1993ab, 1996ab [*Eulemur*]; Passamini, 1998 [*Callithrix*]; Atsalis, 1999a [*Microcebus*]; Gursky, 2000 [*Tarsius*]; Poulsen *et al.,* 2001 [*Lophocebus*]; Gelatt *et al.,* 2002 [*Enhydra*]; Ebensperger and Hurtado, 2005 [*Octodon*]; Hemingway and Bynum, 2005 [*Propithecus*]; Kuntz *et al.*, 2006 [*Equus*]; Tsuji *et al.,* 2006 [*Macaca*]). For instance, sea otters in Alaska spent more time foraging for prey during the winter when sea conditions worsened and prey items declined in abundance and quality (see Gelatt *et al.,* 2002). However, when lumpsuckers were particularly abundant during the winter, feeding time decreased in response to a high quality prey item (Gelatt *et al.,* 2002). This in turn may affect the amount of time devoted to other behaviors involved in energy accumulation, conservation, or expenditure, such as traveling and resting. Therefore, the manner in which an animal adjusts its time budget in response to resource availability can identify biologically significant environmental pressures.

Mammalian time budgets may be differentially affected depending upon a multitude of factors that may interact with food availability, including dietary adaptations, predation risk, reproductive condition, or habitat characteristics, and therefore several solutions to seasonally changing energetic demands may be employed by different species. For instance, a species has multiple options such as whether to

continuously forage as necessity dictates, or to 'stochastically' forage and accumulate reserves for when resources are scarce (Cuthill and Houston, 1997). As with climate, time budgets are typically seen as maximizing energy or minimizing time/energy expenditure.

When resources are scarce, increased time resting may be the only available energetic adjustment option when animals are forced to feed less (*cf* Nash, 1998) and a *time/energy expenditure minimizing strategy* is adopted. In fact, animals may adopt a strategy of decreased travel during the lean season (Boinski, 1987) to minimize time and energy, thereby reducing the amount of nutrients required to maintain energetic homeostasis. Ruminants and the Przewalski horse rely upon energy stores and spend less time feeding during winter when resources are scarce (Kuntz *et al.*, 2006), and feeding time in primates may also decrease during the lean season (*e.g.,* Dasilva, 1992) and in ecologically stressed groups (Dunbar, 1992). While feeding did not decrease in red ruffed lemurs *(Varecia rubra),* this species decreased time spent traveling during the lean season, still effectively adopting a time minimizing strategy (Vasey, 2005). In fact, this pattern is seen in many frugivorous primates (*e.g.,* Terborgh, 1983; Overdorff, 1993a, 1996a; Doran, 1997; DiFiore and Rodman, 2001; Vasey, 2005).

An alternate and widespread pattern during the lean season is an *energy maximizing strategy*, where animals *increase* feeding time and feed on either (A) poorer quality, less digestible foods for longer periods of time, or (B) a large diversity of rare, patchy, high quality foods to accomplish adequate energy intake (Schoener, 1971; Clutton-Brock and Harvey, 1977; Dunbar, 1988; Overdorff, 1988, 1993a, 1996a; Passamini, 1998; Gursky, 2000). For example, golden-mantled ground squirrels spent

2% of their time foraging on herbs during the period of abundance. As the availability of herbs decreased and the diet consisted largely of fungus, time spent foraging increased to 28% (Kenagy *et al.*, 1989).

As predicted by Optimal Foraging Theory (Schoener, 1971), decreased availability of nutrients in the scarce season may also increase travel time or distance as animals adjust to the wider, or less predictable, distribution of food (Barton *et al.*, 1992; Garber, 1993; Overdorff, 1993a; Gursky, 2000). Though rare in primates, many animals including primates (Peres, 1994; Overdorff *et al.*, 1999; Boinski *et al.,* 2005), birds (Morton, 1977; Keuroghlian, 2003), bats (Richter and Cumming, 2006), ungulates (Carrillo *et al.,* 2002), and insects may even migrate to remote areas and establish entirely new home ranges for the duration of the lean season (Hemingway and Bynum, 2005). Food scarcity periods may also be accompanied by cortisol (stress hormone) elevations, which indicate a need for energy mobilization (see Tecot, Chapter 4). These elevations may signify an energetic challenge despite increased time feeding, possibly due to the ingestion of lower quality food, greater energy expended traveling between resources, increased competition, or a suite of interacting factors.

Even when food is abundant, a delicate balance must be maintained to maximize food intake while remaining within metabolic constraints (see Hammond and Diamond, 1997). For example, from humans to insects, increased intake of nutrient-poor foods may cause weight-gain (*e.g.,* Cuthill and Houston, 1997). There is an upper limit to how much food can be stored due to 'mass-dependent' costs, such as elevated metabolic levels during locomotion in heavier mammals (Taylor *et al.*, 1982). Furthermore, Cuthill and Houston (1997) note that increased body mass may also hinder locomotion, increasing

predation risk and anti-predatory behaviors, and thereby foraging efficiency. Thus, several strategies are available to species, but within certain bounds. For instance, a species whose general time budget consists of resting a large majority of the time on average employs a time/energy minimizing strategy. Seasonal environmental changes may be accompanied by time budget modifications which indicate the use of a particular energetic strategy *relative* to the general time budget. Yet, the species may be constrained to continue resting a large majority of the time, and thus the overall strategy of the species may remain the same.

Recent primate studies suggest that an animal's time budget may in fact be largely related to the *nature* of seasonally-induced dietary switching, again highlighting the importance of a species' diet and habitat in determining its time budget. For example, colobus monkeys *(Colobus polykomos)* rest for long periods of time during food scarcity because they mainly subsist upon leaves at this time, which require long periods of rest to accommodate cellulose digestion. During the abundant season they feed for longer periods because they mainly subsist upon seeds, which are easier to digest (Dasilva, 1992).

Habitat Differences

The alteration of a habitat can have a tremendous impact on the type, density, and distribution of plant species, and consequently mammalian time budgets will likely be impacted. Tropical rain forests are characterized by rapid nutrient cycling where plants take up nutrients as soon as they are available, leaving behind very nutrient-poor soil. When trees are extracted from such habitats, nutrients are permanently lost (Ricklefs and

Miller, 2000). Selective logging and fragmentation can also result in smaller, more widely spaced food patches (Balko, 1998), thus requiring more travel or wider group spread while foraging (Irwin, 2007). Long-term studies of species in forests both pre- and post-disturbance are very few in number. Comparative research from different sites with varying habitat disturbance or habitat structure is the ultimate test of how activity might be influenced. As Irwin (2006) states, it is important to identify the nature of flexibility and the extent to which flexibility can be maintained without adverse effects to accurately assess the ability of species to persist in such environments.

Seasonal changes in the feeding ecology of species, as well as overall time budgets, are often variable between sites (Strier, 1986, 1987; Chapman and Chapman, 1999; Hill, 2005; Irwin, 2006; Riley, 2007) due to differences in the local floral and faunal communities, and possibly soil condition (Defler, 1995). Activity budgets in fragmented and continuous forest, or primary and secondary forest, may remain similar (*e.g.,* Onderdonk and Chapman, 2000), yet this is seldom the case (*e.g.,* Irwin, 2006). Beyond their importance for conservation, site comparisons can uncover behavioral flexibilities and identify pressures affecting how animals spend their time and where they put their energy. In a comparison of two studies of muriqui *(Brachyteles)* time budgets, Strier (1987) found that, despite being smaller and more fluid, a group ranging in a less productive forest spent more time feeding and resting and less time traveling (Milton, 1984) than a cohesive group in a forest with large fruit patches (Strier, 1986, 1987). The group in the less productive forest appeared to have adopted an energy maximizing time budget (Milton, 1984; Strier, 1986, 1987). Relative to groups at the other site, these groups also adopted a strategy to conserve time and energy. More time was spent resting

to digest high levels of cellulose and smaller groups allowed individuals to spend less time traveling (Milton, 1984; Strier, 1986, 1987). Teasing apart the numerous potential influences on intraspecific differences is often difficult, particularly when data are collected in different sites at different times by different researchers, sometimes using different methodologies (see Defler, 1995). These types of comparisons have been few in number for this reason. Comparisons of groups in adjacent sites subject to similar climates but different habitat features would more readily facilitate these types of investigations.

The Special Case of Lemurs

The lemurs of Madagascar may possess some interesting differences from other primates since they range in both seasonal and unpredictable climates which differ from other primate habitats. For instance, Madagascar's climate is historically harsh and unpredictable (Ganzhorn *et al.,* 1999b; Wright, 1999), with frequent droughts, cyclones, and frosts (Ganzhorn, 1995a; Sauther, 1998; Wright, 1999; Dewar and Wallis, 1999; Gould *et al.,* 1999), and low soil fertility, slow tree growth (Ganzhorn *et al.,* 1999b), and small tree crown diameter (indicating small patch size) (Ganzhorn *et al.,* 1999a). Eastern Madagascar is subject to high annual levels of rainfall, yet monthly rainfall totals are highly variable (Wright and Overdorff, unpublished data; Tecot, this study). Richard and colleagues (2002) suggest that what little long-term climatic data we have indicate that unpredictability in rainfall is reflected in the phenology of leaves, fruits, and flowers. Lemurs are proposed to have evolved their unique suite of traits in response to this unique environment and the energetic challenges it poses (*e.g.,* Pereira, 1993; Jolly, 1984; Wright, 1999)

As a result, hypotheses regarding distinguishing features observed in various lemurids (*e.g.,* cathemerality, female dominance, small group sizes) suggest adaptations to environmental stress, and predict a direct relationship between climate and reproductive output (*e.g.,* Pereira, 1999; Godfrey *et al.*, 2004; see Wright, 1999). Morland (1993) suggested that since lemurs are characterized by resting metabolic rates lower than that predicted by the Kleiber scaling relationship (Kleiber, 1961; Young *et al.*, 1990), ambient temperature is a particularly important factor for lemurs and may account for island-wide seasonally changing time budgets. In fact, during the cool season several lemur species rest more (Morland, 1993; Schmid and Ganzhorn, 1996; Powzyk, 1997; Schmid, 1998; Wright, 1999), and some *(Microcebus* and *Cheirogaleus)* even enter torpor (see Geiser and Ruf, 1995; Petter-Rousseaux, 1980; Wright and Martin, 1995; Schmid and Kappeler, 1998; Sørg *et al.,* 2003; Dausmann *et al.,* 2004), a behavior generally understood to be an adaptation to enable energy conservation in harsh environments (*e.g.,* Schmid and Stephenson, 2003). These studies implicate thermoregulation, or the avoidance of thermal stress, as at least one potential factor involved in the effect of climate on time budget in lemurs in particular. Therefore, climate may impact a species' energetic input (through its influence on plant reproduction) and/or energetic expenditure and conservation (through its influence on thermal energy exchange) such that the proportion of time devoted to individual behaviors will change between temperature seasons (warm and cool) and rainfall seasons (dry and wet).

As noted above, many primates seasonally adjust their activities, but lemurs may be more flexible than other primates, able to use potentially energy-saving strategies such

as torpor (see above) and activity pattern (nocturnal or diurnal) switching. These have not been widely observed in other primates (see Curtis and Rasmussen, 2006 for an overview of activity pattern switching in New World monkeys *Aotus* and *Alouatta*). While many mammalian species display temporal shifts in the way that activity is distributed throughout the day or night ('activity rhythm'; *e.g.,* Overdorff, 1996b; Sussman, 1974; Strier, 1987; Passamini, 1998; Curtis *et al.*, 1999; Halle and Stenseth, 2000; Vasey, 2004, 2005; Hwang and Garshelis, 2007; Mourão and Medri, 2007), lemurs may be able to extend that daily rhythm over a longer period of time. Overdorff (1996b) found that, similar to some other primates, the activity rhythm of *E. rubriventer* changed between food availability seasons: feeding occurred later in the day and more frequently during scarce resource periods. However, in addition to this seasonal shift in activity rhythm, *E. rubriventer* adopted a cathemeral (day/night active) activity pattern (Overdorff and Rasmussen, 1995; for definitions see Curtis and Rasmussen, 2006, Tattersalll, 1987, 2006) in which the window of activity is extended to 24 hours, as is seen in several microtine species (Halle and Stenseth, 2000). Such extended activity may be influenced by several factors, such as moonlight (Colquhoun, 1998; Curtis *et al.*, 1999; Donati *et al.*, 1999), temperature (Overdorff and Rasmussen, 1995; Fernandez-Duque and Erkert, 2006), precipitation (Curtis *et al.*, 1999; Donati and Borgognini-Tarli, 2006), resource availability (Engqvist and Richard, 1991; Overdorff and Rasmussen, 1995), predation risk (Overdorff, 1988; Rasmussen 1999; Curtis *et al.*, 1999; Colquhoun, 2006; Hill, 2006), or competition (Vasey, 2000) among cathemeral species (Rasmussen, 1999; Overdorff and Johnson, 2003; Curtis and Rasmussen, 2006). For example, Curtis and colleagues (1999) found that mongoose lemur (*Eulemur mongoz)* activity levels shifted

seasonally between day and night. This may be a thermoregulatory response to a seasonally changing body temperature/ambient temperature differential related to environmental temperature and precipitation (Le Maho *et al.*, 1981; Curtis *et al.*, 1999). In this case animals conserve energy by shifting their activity rhythms, and energetic adjustments are made despite a *lack of seasonal changes* in time budget.

Cathemerality may take several forms, however. Rasmussen (1999) suggested that three patterns of cathemeral activity exist in lemurs. While deciduous dry forest-living mongoose lemurs (Pattern A, Curtis and Rasmussen, 2002) shift between predominately diurnal (wet season) and predominantly nocturnal (dry season) activity patterns (Curtis *et al.*, 1999), and seasonally dry forest-living brown lemurs shift from diurnal to 24-hour activity (Pattern B, Curtis and Rasmussen, 2002), rain forest-living lemurs are equally likely to be active throughout all 24 hours of the day throughout the year, with intermittent bursts of activity and sleep (Pattern C, Curtis and Rasmussen, 2002; Overdorff and Rasmussen, 1995; Overdorff and Johnson, 2003; but see Overdorff, 1988). This last pattern is similar to that seen in microtines. For instance, within the 24-hour circadian rhythm, an ultradian rhythm exists where animals are active for bursts of 2-6 hours after which they need to rest (Halle and Stenseth, 2000; Halle, 2006). This may be due to a variety of factors, including digestive needs or the amount of activity necessary to forage (and the subsequent period of rest to recover). Although mongoose lemurs do not seasonally modify time budgets, differences between these two patterns of cathemeral activity, as well as large-scale environmental differences, allow for the possibility of seasonal modifications in the time budgets of lemurs adopting Pattern C versus Pattern A. It has not been determined, however, if and how a cathemeral lemur

adopting pattern C modifies its time budget with temporal variations in climate and resource availability and quality.

Lemurs are also naturally entirely restricted to Madagascar, which has experienced extensive habitat loss mainly from logging and agricultural clearing over the past 2000 years in which humans have occupied the island (Green and Sussman, 1990; Irwin *et al.*, 2005). A coupling of climatic factors and anthropogenic disturbance has created fragmented forests with scarce and unpredictable resources, which affects the density, distribution, and behavior of many lemur species (Harcourt and Thornback, 1990; Dagosto, 1989; White *et al.*, 1995; Johnson and Overdorff, 1999; Grassi, 2001). Because fragmentation causes differential resource distribution and abundance, intraspecific variation in lemur behavior is common across sites (*e.g.,* Harcourt and Thornback, 1990; White *et al.*, 1995; Grassi, 2001). In a study of Diadem sifaka *(Propithecus diadema)* in continuous and fragmented forest in Tsinjaorivo, Madagascar, groups in fragmented forest adopted both energy maximizing and energy/time minimizing strategies when compared with groups in continuous forest (Irwin, 2006). Groups in fragmented forest spent more time feeding and less time resting and traveling, yet during the abundant season groups in different sites were more similar to each other (Irwin, 2006).

Eulemur rubriventer is a largely frugivorous lemur in the eastern rain forests of Madagascar whose behavior is largely known from studies in Vatoharanana, an undisturbed forest in Ranomafana National Park. It is unknown, however, how this species reconciles temporal heterogeneity of resources and climate in a disturbed forest. Simultaneous studies of energy partitioning in populations in disturbed and undisturbed

forest subject to similar climates will demonstrate this species' behavioral flexibility, and identify environmental factors exerting strong selective pressure.

Study Species

This study examines *Eulemur rubriventer,* the red-bellied lemur, to analyze seasonal time budgets and the effects of habitat differences on seasonal time budgets. *E. rubriventer* is an excellent species for this study for several reasons. First, monomorphy (Kappeler, 1991) eliminates the introduction of confounding metabolic- or other size-associated factors (Clutton-Brock *et al.*, 1977; Strier, 1987; Vasey, 2005) that may impact males and females differently. Second, an analysis of the effects of resource seasonality is best conducted with a species whose preferred diet is patchy in time and space, and *E. rubriventer* subsist mainly upon fruit (Overdorff, 1993ab; Tecot, 2007a). Third, a frugivorous diet is also commonly associated with high sensitivity to habitat modification (Johns and Skorupa, 1987; Marsh *et al.,* 1987; Richard and Sussman, 1987; Struhsaker, 1997; Harcourt, 1998), so site differences are also best observed in a frugivorous species. Fourth, rainfall in the eastern rainforests is related to food availability some years, but not in others (Atsalis, 1999a; Overdorff and Wright, unpublished manuscript), thus assisting in interpreting the individual effect of climate on time budget. Fifth, although *E. rubriventer* shift activity rhythms where they are likely to be active at any time during any day of the year (cathemerality, Pattern C) (Rasmussen, 1999; Overdorff and Rasmussen, 1995), they may additionally alter their behavior in response to seasonal changes in food availability (Overdorff, 1996a). Sixth, this species lives in two adjacent sites subject to a similar climate but characterized as different habitat types (see below). Finally, inter-site divergences in time spent traveling may be associated with increased

ranges and resource needs. Group sizes in a species living in family groups are more likely to be similar across sites than group sizes in species with other types of social structures, thus facilitating the study of the impact of the habitat, rather than the impact of group size.

Eulemur rubriventer are at high risk of extinction and are listed as 'vulnerable' on the IUCN Red List (IUCN, 2006). Their range extends along the band of rain forest that runs along eastern Madagascar (Irwin *et al.*, 2005), and has decreased in size since earlier censuses, conducted as recently as 1996 (Mittermeier, *et al.*, 2006). Infant mortality has been estimated to reach as high as 50% (Mittermeier *et al.*, 2006). They live in small, territorial, strictly pair-bonded family groups (Merenlender, 1993; Overdorff and Tecot, 2006), and as a result may be more sensitive to environmental stressors compared with other primates (Hennessy *et al.*, 1995). Both adult males (Overdorff, 1991) and juveniles (Tecot and Overdorff, 2005) carry infants for up to 100 days after birth (Mittermeier *et al.*, 2006). Although most frugivorous species distinguish themselves from folivorous species by remaining active for the majority of the day, red-bellied lemurs display an odd combination of frugivory and extensive bouts of sleeping throughout the day (Overdorff, 1988; Tecot, personal observation).

Predictions

To evaluate the relationships between time budgets and seasonal changes in climate and food availability, this study investigated the behavior of *Eulemur rubriventer* in southeastern Madagascar, throughout fifteen months. To test whether site has an effect on the degree of energetic adjustments necessary, and whether animals are able to make the necessary adjustments to maintain a positive energy balance, this study investigated

time budgets in animals occupying two different tropical rain forest habitats (Talatakely and Vatoharanana) subjected to different degrees of habitat alteration.

***General and Monthly Time Budgets**:* Feeding, resting, and traveling behaviors are predicted to be performed relatively more than grooming, aggression, and playing behaviors because they are directly related to the search, ingestion, and digestion of resources. Time devoted to feeding, resting, and traveling are predicted to fluctuate throughout the year as seasonal environmental changes occur. Although results from Durham (2003) indicate that the amount of time spent feeding by *E. rubriventer* between these sites is not variable, the different levels of fruit availability found in most months in this study suggest that behavioral adjustments may differ. Therefore, groups within each site are predicted to adopt similar general and monthly time budgets, but significant site differences in the amount of time spent performing social, feeding, resting, and traveling behaviors are predicted. Groups in the disturbed site (Talatakely) are expected to spend more time feeding and traveling and less time resting and being social overall, and in each month.

***Climate**:* Climate is predicted to have an effect on time budget. Time budgets are predicted to significantly differ between cool and warm seasons, and between wet and dry seasons. Since *Eulemur* species are less active during the cooler part of the day during the cool season (Curtis *et al.*, 1999; Donati *et al.*, 1999; Rasmussen, 1999; Kappeler and Erkert, 2003; Tarnaud, 2006), *E. rubriventer* are predicted to be less active during the cool season (versus the warm season) to reduce energy expenditure and enable the use of body heat to stay warm. Specifically, lemurs will rest more and feed and travel less than during the warm season.

Since rain and fruit production are not always correlated in Ranomafana National Park (Atsalis, 1999a; Wright and Overdorff, unpublished data), during the wet season *E. rubriventer* are predicted to stay warm during the day by huddling more. Specifically, lemurs will rest relatively more than during the dry season. Because this species is frugivorous, predictions as to its feeding and traveling behavior during the wet season are based upon the time budgets of the frugivorous red ruffed lemur, and feeding is predicted to decrease and traveling is predicted to increase (Vasey, 2005). These patterns will not differ between groups and sites. Since sites are adjacent and subject to the same climate, the strength of the relationship between (1) the amounts of time devoted to feeding, resting, and traveling and (2) temperature and rainfall seasons is not predicted to differ between sites if climate is the only influence upon time budget. Differences in the direction of seasonal behavioral modifications across sites may indicate an interaction between climate and habitat characteristics.

Food Availability*: Eulemur rubriventer* time budgets are expected to differ between scarce and abundant resource seasons. Based upon previous observations of several frugivores, and in particular this species by Overdorff (1996), red-bellied lemurs are predicted to maximize energy and minimize energetic costs during food scarcity, and therefore animals are predicted to feed and rest more and travel less during scarce resource seasons. Increased time resting may also be related to increased time spent feeding upon fibrous foods during the lean season, which may require additional time for digestion. Alternatively, resting will not differ between seasons, as decreased travel and increased feeding may afford animals sufficient energy during the lean season. This pattern is predicted to be the same in all groups and sites. However, since energy

maximization is expected to require greater energy expenditure in the more disturbed site, the differences in time spent performing each behavior across seasons are predicted to be more extreme in the disturbed site.

***Habitat Differences**:* Time budgets are not predicted to vary with group size, as all groups are small (≤ 5 individuals), and therefore the proportion of time spent in each behavior will not differ between groups within sites. General (average) time budgets are, however predicted to differ between sites due to general habitat differences.

As stated above, directional similarities in the time budget response to seasonal changes in climate and resource availability in each site were predicted, as were differences in the strength of these seasonal changes between sites. Here site is predicted to have an effect on the *timing* of changes in time budgets, so time spent feeding, resting, and traveling should significantly differ between sites on a monthly basis. Furthermore, the amount of time devoted to feeding, resting, and traveling behaviors are predicted to significantly differ between sites within each climate and fruit season.

Since frugivores typically spend more time feeding when resources are scarce, and more time resting in order to digest lower quality resources, lemurs in the more disturbed forest, Talatakely, are predicted to spend more time feeding and resting in all climate seasons and fruit scarce seasons. When fruit is abundant, animals in Talatakely will still be required to spend relatively more time feeding than animals in Vatoharanana since fruit is not as abundant in that site, but the need to rest for longer periods in order to digest cellulose will not be necessary. Instead, groups in Talatakely are predicted to spend relatively more time traveling during fruit abundance as they travel between food patches than groups in Vatoharanana.

METHODS

To determine the effects of climate, food availability, and habitat on time budget, this study examined five *Eulemur rubriventer* (red-bellied lemur) groups in Ranomafana National Park, Madagascar. Two groups were studied in a high-altitude primary rain forest (Vatoharanana), and three groups were studied in a low-altitude secondary rain forest (Talatakely). Data were collected January 2004-March 2005 (n=2586 hours).

Sites

Data were collected in Ranomafana National Park (RNP) which consists of approximately 43,500 ha of evergreen rain forest in Fianarantsoa Province, southeast Madagascar (between 21˚02' to 21˚25' S and 47˚18' to 47˚37' E) (DuPuy and Moat, 1995). This park contains the largest known population of *Eulemur rubriventer* (Wright 1992), as well as at least 11 other primate taxa (Wright, 1992). RNP ranges from lowland forest (500m) to montane rain forest (1500 m) and is highly seasonal with large peaks and prolonged troughs in food availability, particularly fruit (Hemingway, 1995; Morland, 1991; Overdorff, 1993a, 1996a; Overdorff and Strait, 1998; Wright, 2007; Tecot, Chapter 2). The amount of rainfall (avg. 1500 mm – 4000 mm per year) and the lengths of wet and dry seasons display extreme inter-annual variability (Overdorff and Wright, unpublished manuscript; Wright 1992). Cyclone activity typically occurs January through March. Phenological patterns are highly unpredictable from year to year, with the availability of fruits, flowers, and new leaves varying dramatically (Wright *et al.,* 2005; Wright, 2006; Overdorff and Wright, unpublished manuscript).

Within RNP, data were collected in two adjacent study sites, Talatakely and Vatoharanana, each with an established and maintained trail system (White *et al.*, 1995,

Wright, 1997). The density and abundance of plant species (including those resources preferred by the lemur population) differ between these sites (Tecot, Chapter 2) as a result of selective logging (Balko, 1998; Turk, 1995; Wright, 1995).

Talatakely: Located near the park entrance at 500m in altitude, this site was heavily logged from 1986 to 1989 and is currently regenerating. As a result of habitat alteration, this site is characterized by secondary rain forest with large stands of non-native Chinese guava (*Psidium* spp.), emergent non-native *Eucalyptus* trees (Overdorff, 1988), a discontinuous tree canopy, lower tree species diversity, and trees smaller in diameter at breast height (dbh), height, and crown volume than those in Vatoharanana (Table 3.1) (White *et al.*, 1995; Balko, 1998; Tecot, Chapter 2). The understory largely consists of Rubiaceae and Myrsinaceae, bamboo, and epiphytic species (Turk, 1995). Research at this site was conducted within the 5 km^2 trail system.

Vatoharanana: This site is located 6 kilometers south of Talatakely, at approximately 1200m in altitude. Although this site was selectively logged and approximately 1,000 trees were removed (Balko, 1998), it is characterized by continuous primary forest with steep mountain slopes, greater tree diversity, a more continuous canopy, and trees larger in dbh, height, and crown volume than those in Talatakely (Table 3.1) (Balko, 1998; Overdorff, 1988; White *et al.*, 1995; Tecot, Chapter 2). This site also contains some tree species exploited by *Eulemur rubriventer* which are not present in Talatakely (Tecot, Chapter 2). Research at this site was conducted within the 6 km^2 trail system, as well as an extended trail system constructed during this study and previously by S. Karpanty.

These sites are ideal for this study because they have experienced differential habitat disturbance, yet are subject to similar climates (rainfall and temperature), facilitating inter-site comparisons without the potentially confounding influence of climatic differences.

Table 3.1. Forest characteristics for study sites in Ranomafana National Park. Data were collected September 2003, except where indicated. Significant results are denoted by asterisks. Higher results are bolded.

Characteristic	**Talatakely (heavily logged)**	**Vatoharanana (selectively logged)**
Mean Diameter at Breast Height (cm) ± SD (N)***	7.10 ± 6.62 (873)	**11.25 ± 12.17 (539)**
Mean Tree Height (m) ± SD (N)**	8.57 ± 5.01 (884)	**9.63 ± 6.55 (542)**
Mean Crown Diameter (m) ± SD (N)	**2.59 ± 2.15 (886)**	2.47 ± 2.06 (542)
Mean Crown Depth (m) ± SD (N)**	3.09 ± 2.54 (886)	**3.19 ± 3.29 (542)**
Mean Crown Volume (m^3) ± SE[1]	198.52 ± 37.63	**238.73 ± 16.68**
Mean Basal Area (m^2) (N)***	0.007 (873)	**0.02 (539)**
Total Basal Area/ha (m^2) (N), CV	33.21 (873), 0.329	**71.31 (539), 0.326**
Species Richness (N)	113 (973)	**123 (630)**
Evenness (N)	0.85 (973)	**0.88 (630)**
Shannon & Wiener Diversity Index (N)		
Site Species Diversity	4.02 (973)	**4.21 (630)**
Site Structural Diversity	4.75 (226)	**4.84 (264)**
Simpson Diversity Index (N)[2]		
Site Species Diversity	0.970 (973)	**0.980 (630)**
Site Structural Diversity	0.990 (226)	**0.991 (264)**

[1]Crown Volumes from Balko, 1998. Shannon-Weiner Diversity Index (H)=Σ (pi) (ln pi), where pi=relative density of the ith species, is a measure of species diversity.
[2]Simpson Diversity Index: A lower score indicates more diversity.

Subjects

Eulemur rubriventer adults weigh approximately 1.55-2.21 kg (Glander *et al.,* 1992; Terranova and Coffman, 1997; Tecot, unpublished data). The diet of *E. rubriventer* is composed mainly of fruits and leaves, and supplemented with flowers, nectar, fungus, bark, dirt, and insects (Overdorff, 1988, 1991, 1993ab, 1996ab; Overdorff and Tecot, 2006; Tecot and Overdorff, 2006; Tecot, 2007a). Within Ranomafana National Park, *E. rubriventer* groups range in both disturbed and undisturbed forests. Densities within the park have been estimated to be anywhere from 5 to 19 individuals per km^2 (Overdorff, 1991; Grassi, 2001; Irwin *et al.*, 2005). Mating generally occurs in May, and parturition occurs in September; infants complete weaning December through March.

This study analyzes behavioral data collected from adults and juveniles (n=17; data collected on infants *ad libitum*) in five groups (n_{Vato}=2 groups; n_{Tala}=3 groups) of *E. rubriventer* (Table 3.2). Individuals were identified by distinctive sexually dichromatic markings such as patches of white skin under the eyes of males or a white ventrum on females, or colored collars with tags.

Table 3.2. Group compositions. Demography for groups in Vatoharanana (groups 1 and 2) and Talatakely (groups 3-5) throughout the 19-month study.

Group ID	# adult females	# adult males	# infants and juveniles	# immigrations	# emigrations	# deaths	# hours observation
1	1	1	3	0	0	1	730
2	1	1	2	0	0	0	696
3	1	1	1	1	1[1]	1[1]	361
4	1	1	2	0	1	2	388
5	1	1	3	1	1	2	411
Total	**5**	**5**	**11**	**2**	**2-3**	**4-5**	**2586**

[1] Emigrated or died.

Data Collection

Climate

To test the predictions related to climate seasonality, temperature and rainfall were used as indices of climatic change (see Chapter 2). In each site minimum and maximum temperatures were recorded in degrees Celsius each day and rainfall was collected in a rain gauge and measured in millimeters each morning, or in the case of high rain volume, when full throughout the day.

Phenology

To test the predictions related to food availability and site differences, phenological assessments were made at each site according to the methods in Overdorff (1991, 1996a) (see Chapter 2). Three botanical plots (100 x 10, 5 x 50, and 10 x 25) were

established at each site within known *Eulemur rubriventer* home ranges (highland, slope, and valley). Initially, all trees and lianas 2.5 cm diameter at breast height (dbh) or larger (n=1674) were marked and identified by common Malagasy name with the help of local research technicians. Later species designations were determined using published work by Overdorff (1991), Turk (1995), and the Missouri Botanical Garden database. The availability of fruits (ripe, unripe), flowers (buds, blooms), and leaves (immature, mature) was recorded for each marked tree on a scale of 0 (absent) to 5 (full abundance) each month (Oates, 1977; Overdorff, 1996a).

Behavior

To estimate an overall time budget for the red-bellied lemur, 17 behaviors in 6 categories were recorded (Table 3.3). Though the category 'Aggression' consisted of events, the entire aggressive interaction was recorded as a series of events, the whole of which composed a state with duration. All occurrences of aggressive, feeding, grooming, resting, traveling, and playing behaviors in focal individuals were recorded continuously for eight hours per day (within 0700-1600), 5 days per week, rotating focal animals daily. Each time a behavior occurred, the following data were recorded:

1. Date
2. Focal animal
3. Start Time
4. End Time
5. Director
6. Behavior

7. Receiver

Data were collected at both sites January 2004-March 2005 (15 months). Since red-bellied lemurs are cathemeral (Overdorff, 1988; Overdorff and Rasmussen, 1995; Tecot, personal observation), it is not possible to locate groups in the previous evening's sleeping tree. Due to the difficulty in finding groups, and despite every attempt to be consistent, beginning data collection at the same time each day was not always possible. Therefore, data were collected for up to eight hours per day (0700-1600). Due to their cathemeral activity pattern, slight differences in daily start times were not as problematic as in other studies when additional data collection while animals are in sleeping trees can have a large effect upon results. Time budgets were based upon 2586 hours of continuous focal animal sampling (Altmann, 1974), and were compiled for each adult and juvenile individual (n=17). Weekly mean proportions of time each individual devoted to each behavioral category from January 2004 – March 2005 were combined to construct time budgets for each site (n=2), group (n=5), and the species in general (see Data Analysis below).

Table 3.3. Behavioral categories. All recorded behaviors were assigned to one of six behavioral categories for data analysis.

Aggression	Grooming	Feeding	Resting	Playing	Traveling
Bite	Allogroom	Feed	Resting	Self Play	Move (within 1 tree)
Cuff	Autogroom	Drink		Mutual Play	Travel
Lunge	Mutual Groom	Sniff		Play Bite	
Chase				Play Jump	

Data Analysis

A general time budget was calculated by pooling data collected from all individuals between January 2004 and March 2005 to yield a total time spent in each behavior. Although data collection was not evenly distributed across individuals, a Mixed Model found no differences between the sexes in time spent in each behavior (feeding: $F(1,112.795)=2.172$, $p=0.143$; resting: $F(1,209.246)=0.355$, $p=0.552$; traveling: $F(1,164.905)=0.024$, $p=0.876$).

Behaviors were divided into subcategories (Table 3.3) and the amount of time spent performing each behavior was expressed as the proportion of total time observed. For group and site comparisons the total time each group or site performed a behavior was divided by the total time each site or group was observed. Time budgets were calculated overall and monthly. Months are numbered consecutively 1 through 15; months 1 through 12 represent January through December 2004 and months 13 through 15 represent January through March 2005.

Monthly temperature means were used to determine cool and warm seasons and monthly rainfall totals were used to determine dry and wet seasons. No differences

between sites were found and data were pooled. Daily temperature means were calculated by averaging minimum and maximum temperatures in each site. To calculate monthly means, daily temperature means were added and divided by the number of days in the month. Temperature data from both sites were pooled by adding monthly means and dividing by the number of sites (2). Monthly rainfall was calculated by adding total rainfall collected each month in each site and dividing by the number of sites. Where rainfall was missing, the total rainfall for the month was divided by the number of days data were recorded, and then multiplied by the total number of days in the month, for an estimate of monthly total rainfall. During this study, the drier season in these two sites (73.56 mm – 300.39 mm rainfall per month) occurred between April and November, with a nadir September-October, and the wetter season (345.66mm – 701.41mm rainfall per month) occurred between December and March. Since these sites are located in the tropics where temperature fluctuations are mild, cool and warm season delineations were based upon small incremental changes in temperature. The cooler season (15.14˚C – 17.16˚C) occurred between May and September, and the warmer season (17.91˚C – 19.81˚C) occurred between October and April (Figure 3.1). These results are similar to those reported in Hemingway and Overdorff (1999), where the cooler-drier season occurred May-November and the warmer-wetter season occurred December through April.

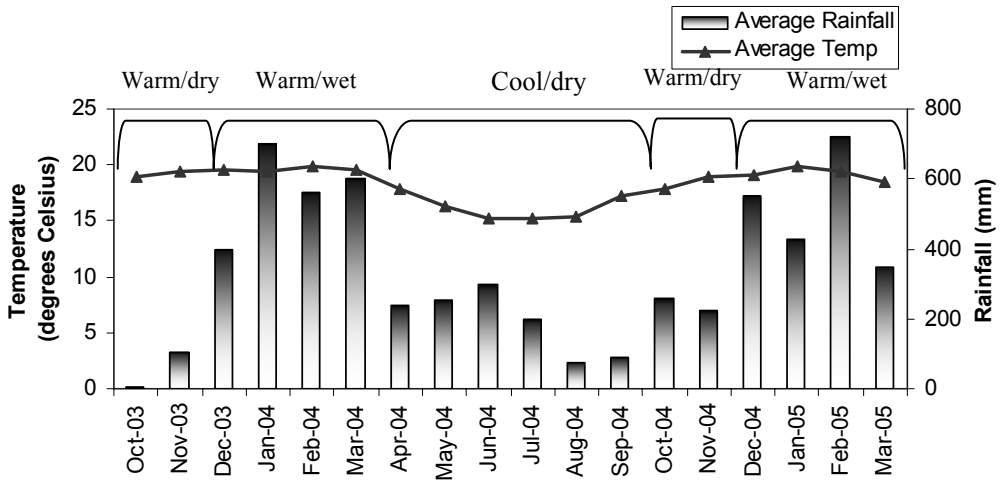


Figure 3.1. Monthly mean rainfall (mm) and total temperature (˚C). The cool season was May-September; the warm season was October-April. The dry season was April-November; the wet season was December-March.

Food availability seasons were determined by totaling the number of trees and lianas with a score of 1-5 for each food item in each phenophase, and dividing by the total number of trees and lianas assessed each month in each site. 'Food abundance' was determined Food abundance and scarcity seasons did not coincide with previous studies (see Overdorff and Tecot, 2006; Tecot, Chapter 2), and differences between sites were apparent. Mature leaves were abundant throughout the year with no fluctuation in availability, so although they were a food source they were not used to show fluctuations in food availability.

Results drastically differed depending upon how resources were combined for analysis due to the much higher abundance of unripe fruit during ripe fruit scarcity or absence (Tecot, Chapter 2). For instance, when unripe fruit is viewed alone or in combination with ripe fruit in Talatakely, March is a period of abundance (Figure 3.2). However, no ripe fruit was present at this site in March (Figure 3.2). Therefore, since

both ripe and unripe fruit may be important components of the diet, yet their nutritional values may differ and affect time budgets differently, food availability seasons were analyzed in two ways: by total fruit availability and by ripe fruit availability (which will allow investigation of the impact of unripe fruit as well) (Figures 3.2 and 3.3). Resource availability seasons for each site are summarized in Table 3.4.

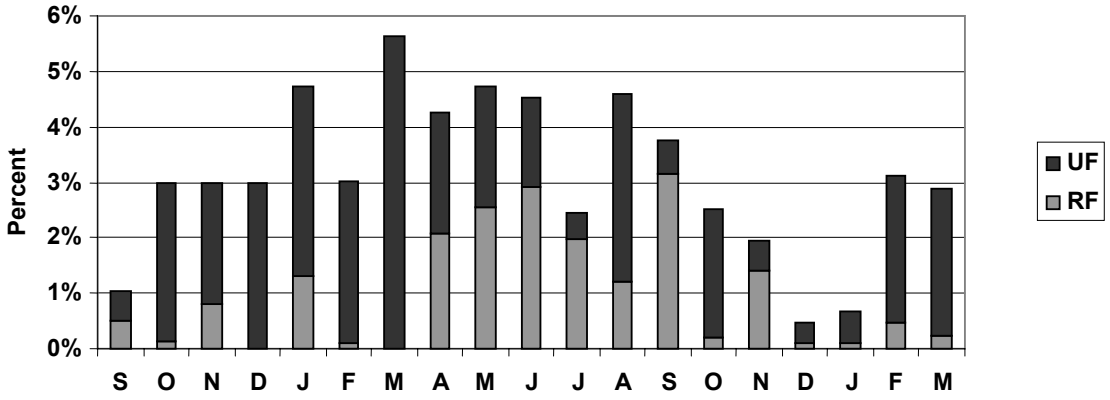


Figure 3.2. Fruit availability in Talatakely. Proportion of trees in Talatakely (disturbed habitat) botanical plots with scores of 1-5 for ripe (gray)or unripe (black) fruit each month. Note difference in y-axis scale compared with Figure 3.3.

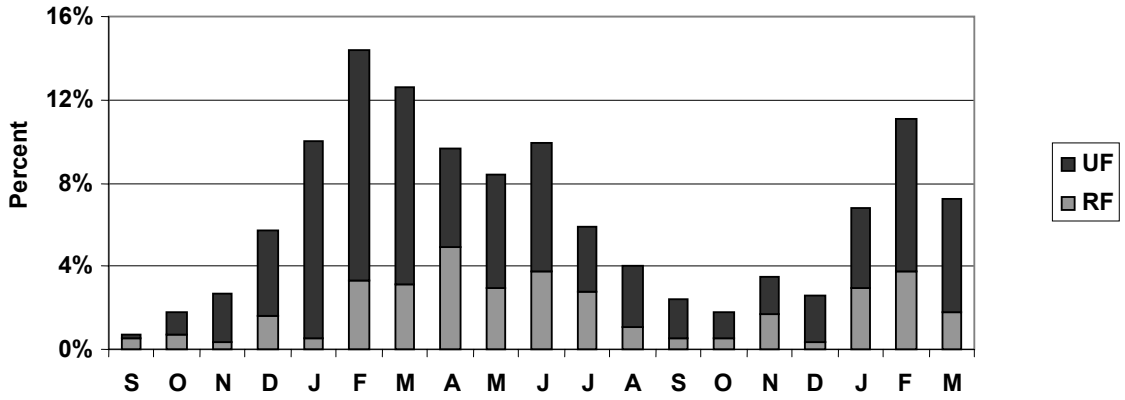


Figure 3.3. Fruit availability in Vatoharanana. Proportion of trees in Vatoharanana (undisturbed habitat) botanical plots with scores of 1-5 ripe (gray)or unripe (black) fruit each month. Note difference in y-axis scale compared with Figure 3.2.

Table 3.4. Food abundance and scarcity seasons in Talatakely and Vatoharanana in Ranomafana National Park, Madagascar between January 2004 and March 2005. Consecutive month numbers represent each consecutive month of the study, beginning in January when behavioral data collection commenced. Abundance and scarcity seasons were determined by the availability scores of ripe fruit and the combination of ripe and unripe fruit in botanical plot trees. Ripe fruit abundance occurred when ripe fruit was present on ≥2% of monitored trees; Total fruit abundance occurred when ripe or unripe fruit was present on ≥2.5% of monitored trees.

Site	**Ripe Fruit Abundance Months**	**Ripe Fruit Scarcity Months**	**Total Fruit Abundance Months**	**Total Fruit Scarcity Months**
Talatakely	1, 4-7, 9, 11	2-3, 8, 10, 12-15	1-6, 8-9, 14-15	7, 10-13
Vatoharanana	2-7, 13-14	1, 8-12, 15	1-7, 13-15	8-12

Seasonal time budgets were calculated using data collected between January 2004 and March 2005 (15 months, 74 weeks). Despite efforts to collect data evenly across individuals, groups, and sites, this was not possible. Because data were collected unevenly amongst individuals, groups, and sites, the total time each individual, group, and site performed each category of behavior each week or month (see below) was divided by the total time each individual, group, and site was observed each week or month. Data were pooled by week to see if there was an effect of climate on time budget. Weeks were numbered 1 through 74 and classified as either 'dry' or 'wet' for rainfall season, or 'cool' or 'warm' for temperature season.

Data were pooled by month to see if there was an effect of food availability on time budget since phenological assessments occurred monthly and therefore did not change on a weekly basis. Months were numbered 1 through 15 (see above) and classified as either 'scarce' or 'abundant'.

To analyze general time budgets and to test the effects of seasons on time budgets, a General Linear Model using a Mixed Model procedure was employed and used to construct a least squares model. Multi-level modeling accounts for inter-individual variation and repeated measures. Data were analyzed with SPSS 15.0 Program for Windows. Effects are considered statistically significant at $p<.05$. Significance is denoted using standard notation: * $P<.05$; ** $P<.01$; *** $P<.001$ (Sokal and Rohlf, 1981).

RESULTS

General Time Budget

All individuals combined spent the majority of their time resting and aggression was extremely rare (Figure 3.4). The amount of time devoted to each behavior significantly differed from the amount of time devoted to all other behaviors, $F(5,796)=2937.18$, $p<.001$ (Figure 3.5). The high percentage of time devoted to resting may be attributed to either higher activity levels at night, or an overall time/energy minimizing strategy.

In a Mixed Model of behavior by month with fixed factor month, repeated by week, feeding, resting, and traveling behaviors differed significantly across months (Feed: $F(14,49.52)=24.637$, $p<.001$; Rest: $F(14,38.20)=10.636$, $p<.001$); Travel: $F(14, 32.82)=4.933$, $p<.001$ (Figures 3.6, 3.7, and 3.8), indicating time budget adjustments throughout the year.

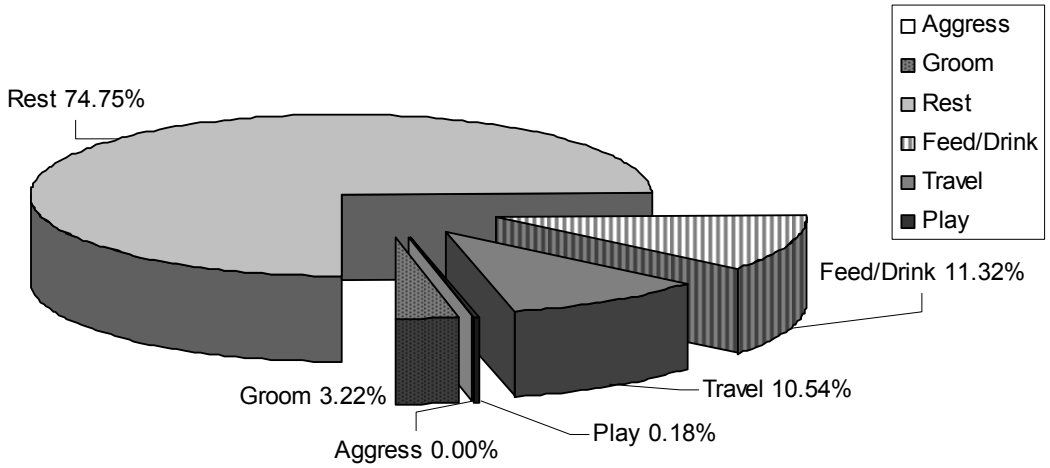


Figure 3.4. Mean general time budget for red-bellied lemurs *(Eulemur rubriventer)* in Ranomafana National Park, Madagascar from January, 2004 through March, 2005.

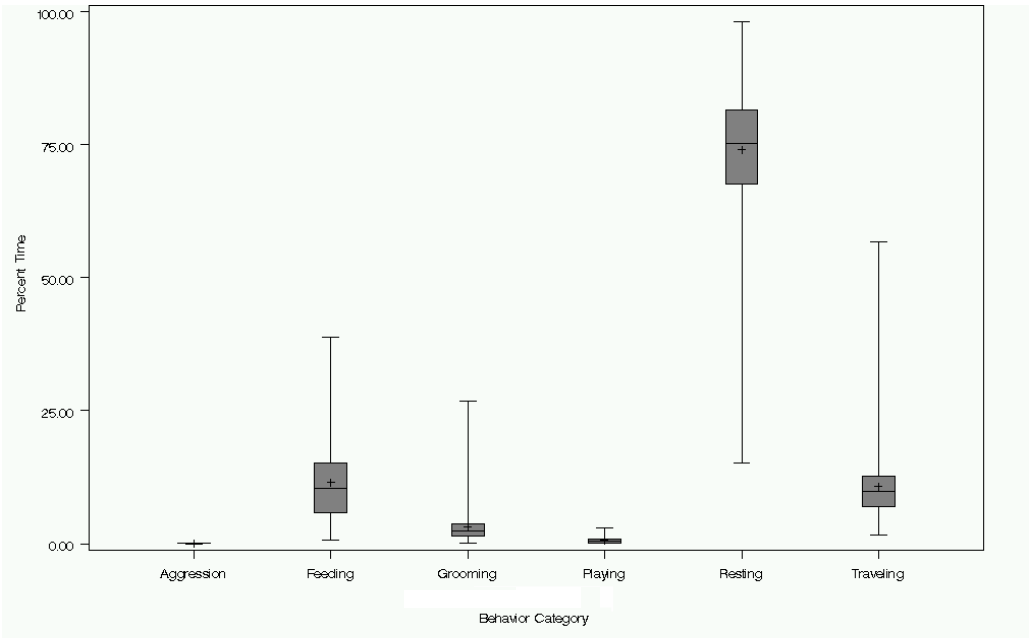


Figure 3.5. Mean general time budget boxplot for all groups. Proportions calculated from weekly means. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data. The relative amount of time spent performing each activity significantly differed from time spent performing all other activities, $p<.001$.

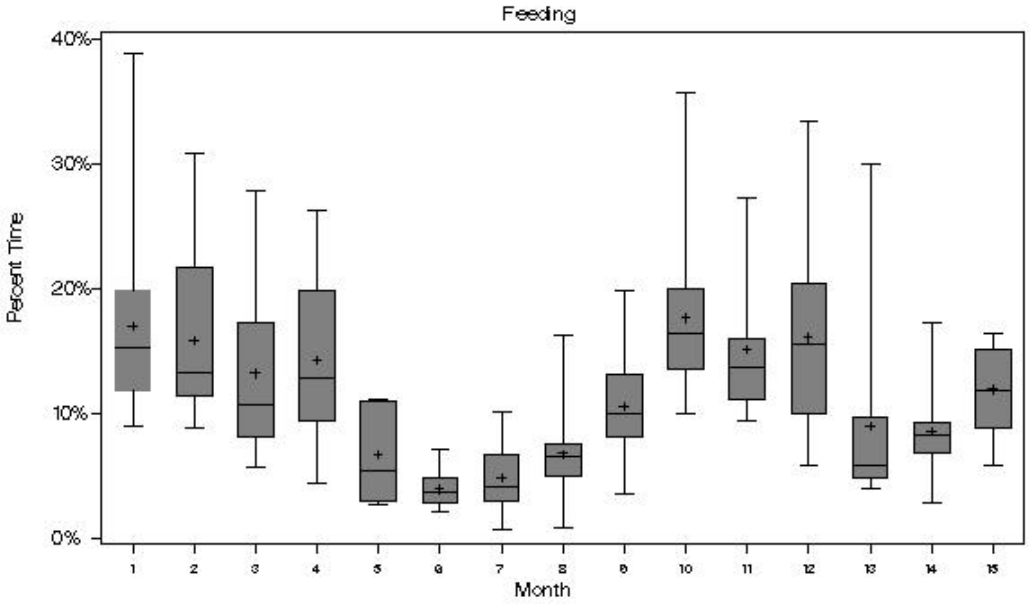


Figure 3.6. Boxplots of relative time spent feeding each month. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data.

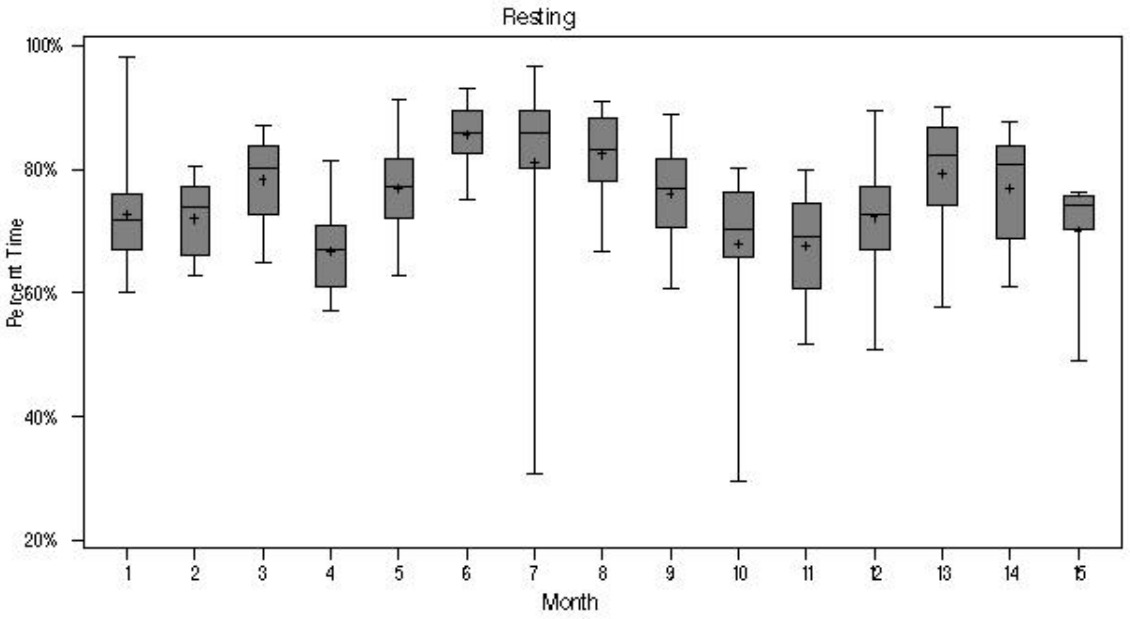


Figure 3.7. Boxplots of relative time spent resting each month. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data.

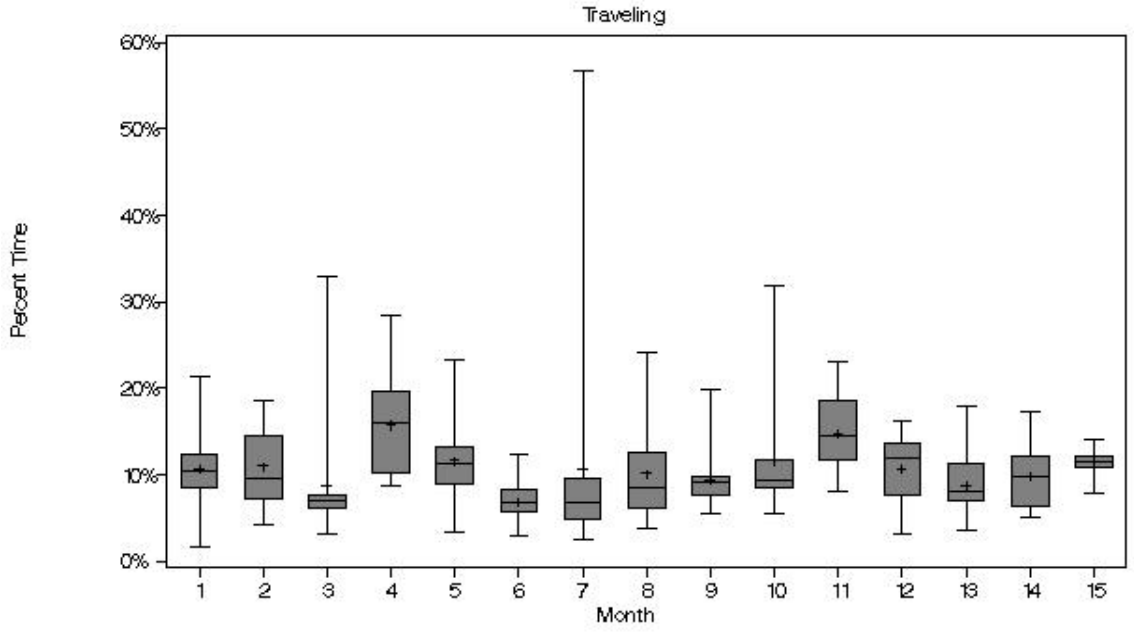


Figure 3.8. Boxplots of relative time spent traveling each month. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data.

Sites

As predicted, general time budgets differed significantly by site. Compared with groups in Vatoharanana, groups in Talatakely rested significantly more overall, $F(1,86.80)=8.990$, $p<.01$, and spent relatively less time engaged in social behaviors (agonism, playing, grooming), $F(1,224.30)=19.918$, $p<.001$ (Table 3.5). However, unexpectedly, travel did not differ between sites, $F(1,159.25)=0.275$, $p=0.601$, and groups in Talatakely fed significantly *less* than groups in Vatoharanana, $F(1,225.12)=34.445$, $p<.001$ (Figure 3.9).

As predicted, time budget *patterns* throughout the year were similar at both sites, yet monthly time budgets differed. Using a Mixed Model with fixed effects month and

site for each behavior, significant differences in feeding, resting, and traveling were found between sites. In Talatakely less time was spent feeding during most months (Figure 3.10), and differences between sites in the amount of time spent resting and traveling depended upon the time of year (Figures 3.11 and 3.12). Months in which all three behaviors significantly differed between sites were 9, 11, and 13. Detailed results of these findings (by behavior, below) identify when these differences were most apparent.

The timing and duration of peaks and troughs in feeding behavior varied between sites. Peaks in time spent feeding throughout the study were prolonged in Vatoharanana, and troughs were prolonged in Talatakely (Figure 3.10). There was a significant effect of site on feeding by month, $F(14,38.69)= 3.484$, $p<.001$. Contrary to predictions, less time was spent feeding in Talatakely in all significantly different months (n=6), as well as almost all other months (Figure 3.10).

The timing and duration of peaks and troughs in resting behavior varied between sites. Resting troughs (long periods of relatively little rest) were prolonged in Vatoharanana; peaks were somewhat prolonged in Talatakely (Figure 3.11). There was a significant effect of site on resting by month, $F(14,32.75)=4.364$, $p<.001$, with significant differences between sites in 4 months. Contrary to predictions, time spent resting in Talatakely was significantly higher in three of the months in which significant differences were found (Figure 3.11).

The timing and duration of peaks and troughs in traveling behavior varied greatly between sites, as well as from month to month within sites (Figure 3.12). There was a significant effect of site on traveling by month, $F(14,29.44)=7.223$, $p<.001$, with

significant differences between sites in six months. Although time spent traveling was predicted to be higher in Talatakely, this proved true in only half of the months in which significant differences were found (Figure 3.12).

Table 3.6 displays the parameter estimates, standard errors, F-values, and corresponding p-values obtained from pairwise comparisons based upon estimated marginal means for each significant finding for monthly site differences in (A) feeding, (B) resting, and (C) traveling.

Table 3.5. Mean general time budgets (proportion of total time observed) for five groups of *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar from January 2004 through March 2005.

Site	**Group**	**Group Size**[1]	**Feed**	**Rest**	**Social**	**Travel**
Vatoharanana (selectively logged)	Group 1	4	12.04	72.75	3.32	11.89
	Group 2	3	13.28	73.48	4.17	9.07
Vatoharanana Means			12.65	73.11	3.74	10.51
Talatakely (heavily logged)	Group 3	2	8.51	79.60	3.07	8.81
	Group 4	5	8.14	79.14	2.96	9.76
	Group 5	2	12.10	71.93	2.94	13.04
Talatakely Means			9.72	76.75	2.97	10.56

[1] Group sizes exclude infants and reflect the most common size of each group for each day of the study.

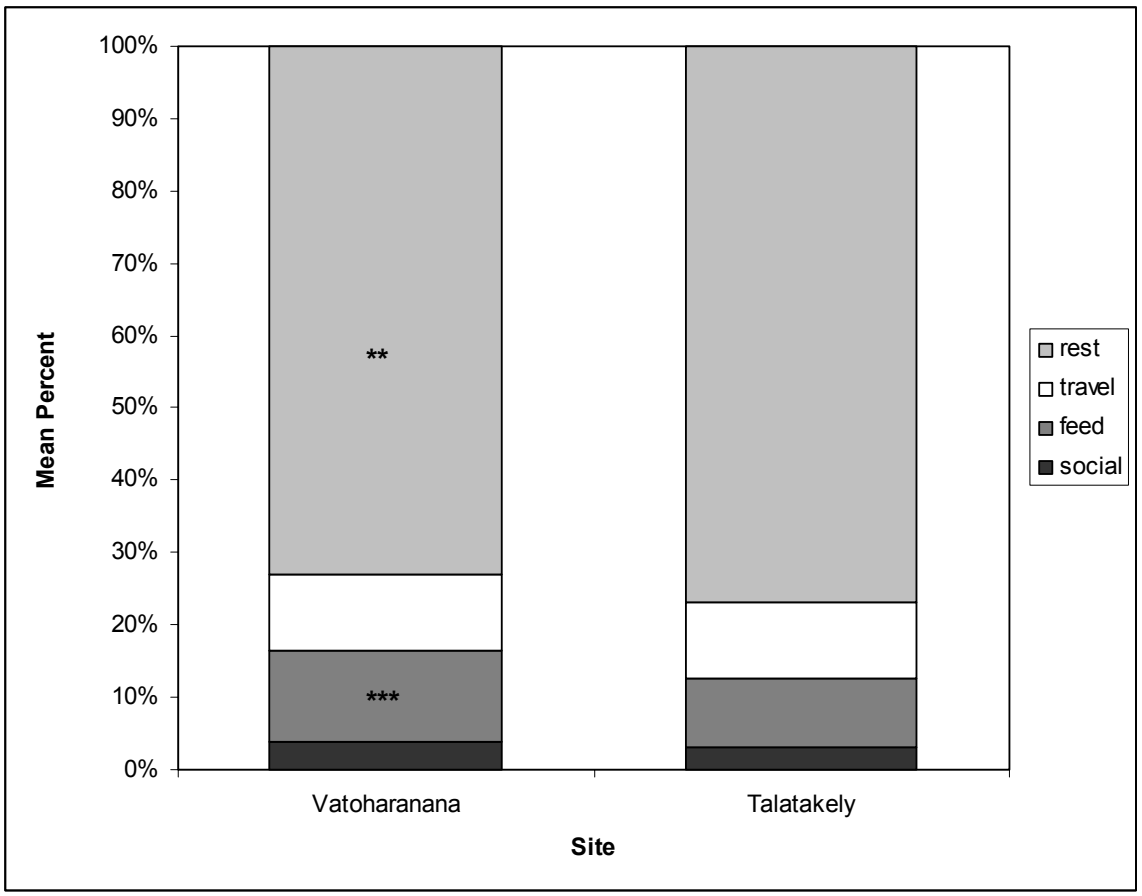


Figure 3.9. General time budget for each site. Feeding and resting differed significantly between sites.

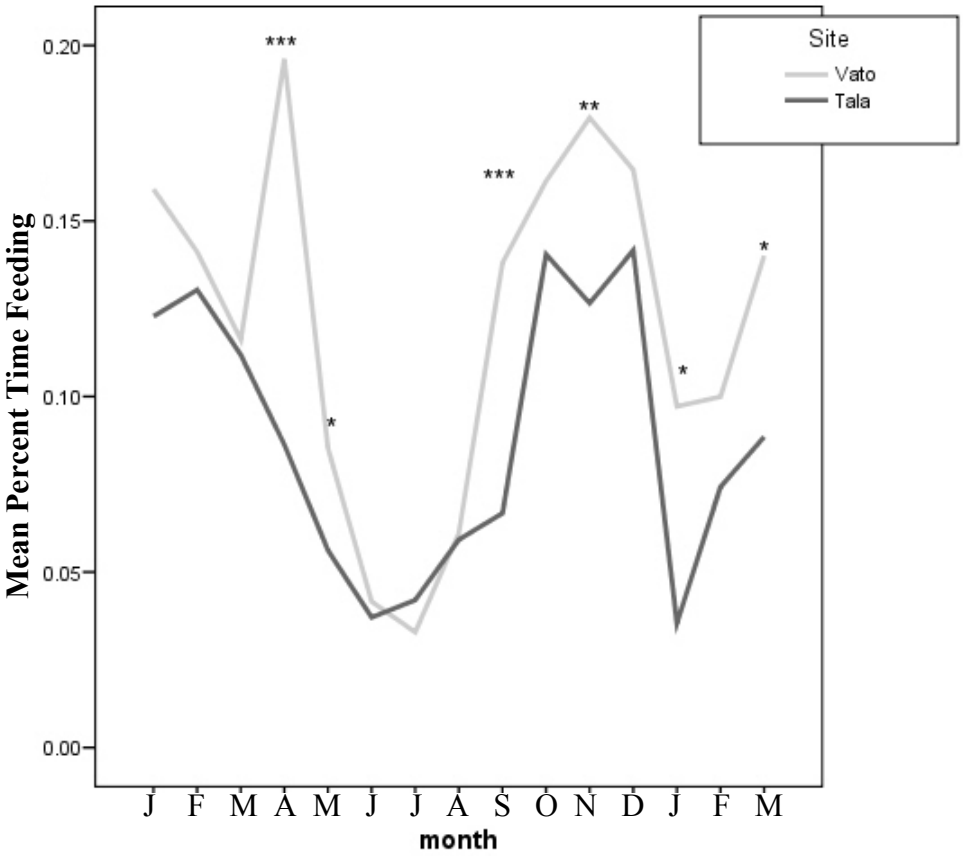


Figure 3.10. Mean values for proportion of time spent feeding at each site throughout fifteen months. Time devoted to feeding differed significantly between sites during April, May, September, and November, 2004 and January and March, 2005.

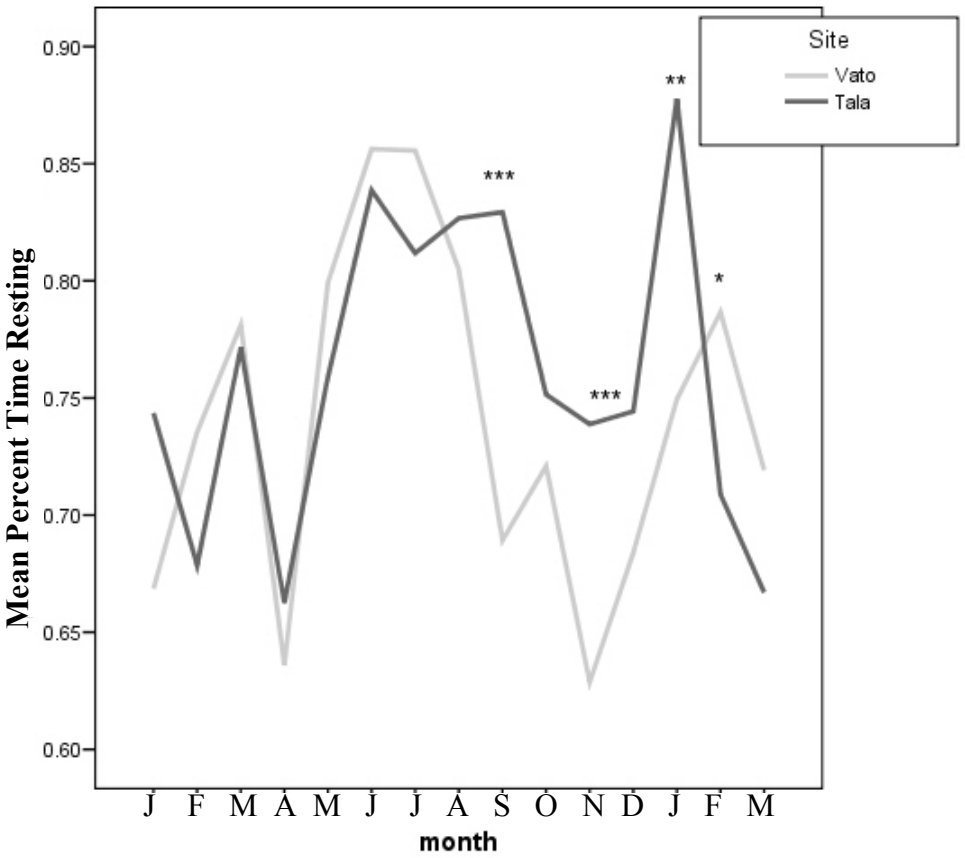


Figure 3.11. Mean values for proportion of time spent resting at each site throughout fifteen months. Time devoted to resting differed significantly between sites during September and November, 2004, and January and February, 2005.

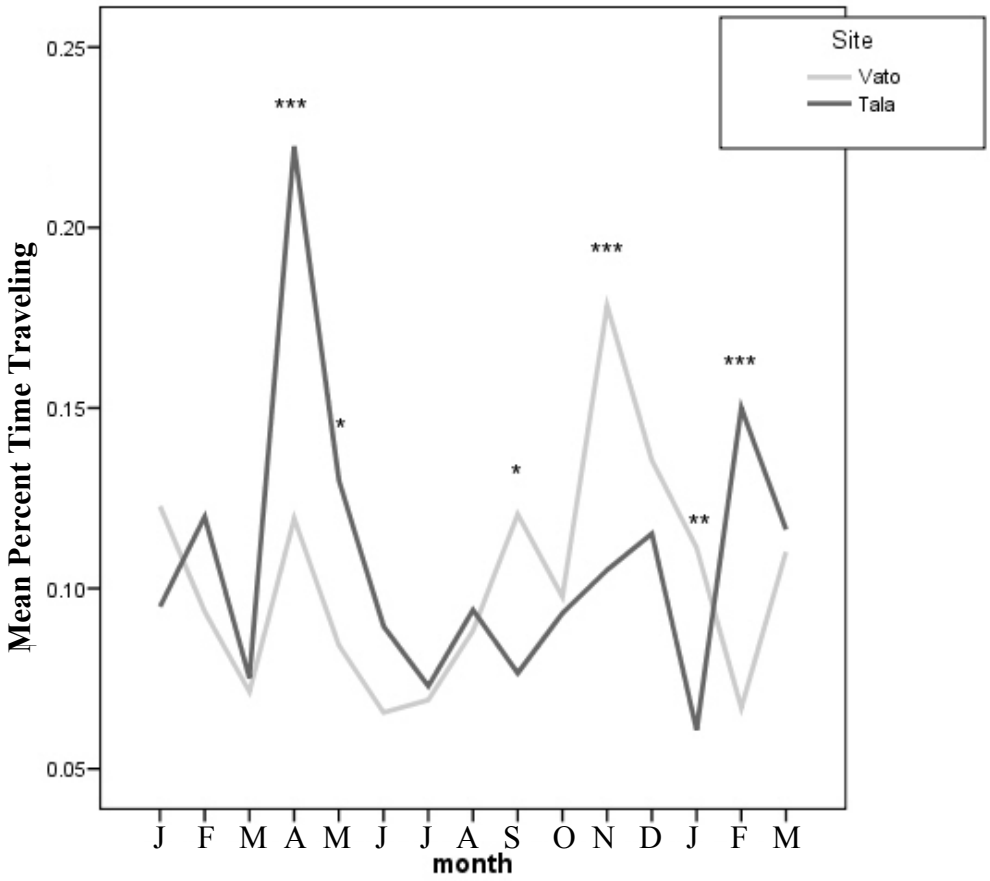


Figure 3.12. Mean values for proportion of time spent traveling at each site throughout fifteen months. Time devoted to traveling differed significantly between sites during April, May, September, and November, 2004, and January and February, 2005.

Table 3.6 Parameter estimates for monthly site comparisons in (A) feeding, (B) resting, and (C) traveling. Months are listed if significant differences in time spent feeding were found among sites.

(A) Feeding

Month	Standard Error	F-value	Numerator df	Denominator df	P-value
4	0.020	30.129	1	21.39	***p <0.001
5	0.014	4.304	1	24.82	*p <0.05
9	0.016	19.506	1	18.78	***p <0.001
11	0.019	7.983	1	24.41	**p <0.01
13	0.022	8.204	1	14.70	*p <0.05
15	0.023	5.203	1	18.85	*p <0.05

(B) Resting

Month	Standard Error	F-value	Numerator df	Denominator df	P-value
9	0.032	18.972	1	27.674	***p <0.001
11	0.025	19.438	1	24.219	***p <0.001
13	0.037	12.061	1	21.563	**p <0.01
14	0.030	6.935	1	23.916	*p <0.05

(C) Traveling

Month	Standard Error	F-value	Numerator df	Denominator df	P-value
4	0.026	16.089	1	20.16	***p <0.001
5	0.017	7.013	1	9.85	*p <0.05
9	0.017	6.522	1	26.10	*p <0.05
11	0.013	31.270	1	19.18	***p <0.001
13	0.017	8.498	1	21.59	**p <0.01
14	0.017	24.021	1	32.55	***p <0.001

Groups

As food sources in groups' ranges differed spatiotemporally, the top three behaviors (feeding, resting, and traveling) were further analyzed by group (Figure 3.13). Groups differed significantly in the amount of time devoted to feeding, $F(4,829)=4.36$, $p<.001$ (Figure 3.14) and resting, $F(4,829)=15.53$, $p<.01$ (Figure 3.15), and traveling approached significance, $F(4,829)=2.28$, $p=0.0591$ (Figure 3.16). The large variance in proportion of time spent traveling in group 4 is notable, and coincides with data indicating larger day and home ranges for this group (Tecot, in preparation). Pairwise comparisons revealed that all significant differences in feeding and resting were between groups at different sites, with the exception of group 5 from Talatakely, which more closely resembled groups from Vatoharanana (Table 3.7, Figure 3.17).

Group 5 in Talatakely was exceptional for several reasons, and results from this group should be viewed with caution. Group 5 underwent several changes in group composition in the beginning of this study, including death, emigration, and immigration

in March/April 2004. This group also ranged almost entirely in guava, and frequented the nightly banana feedings by tourist guides.

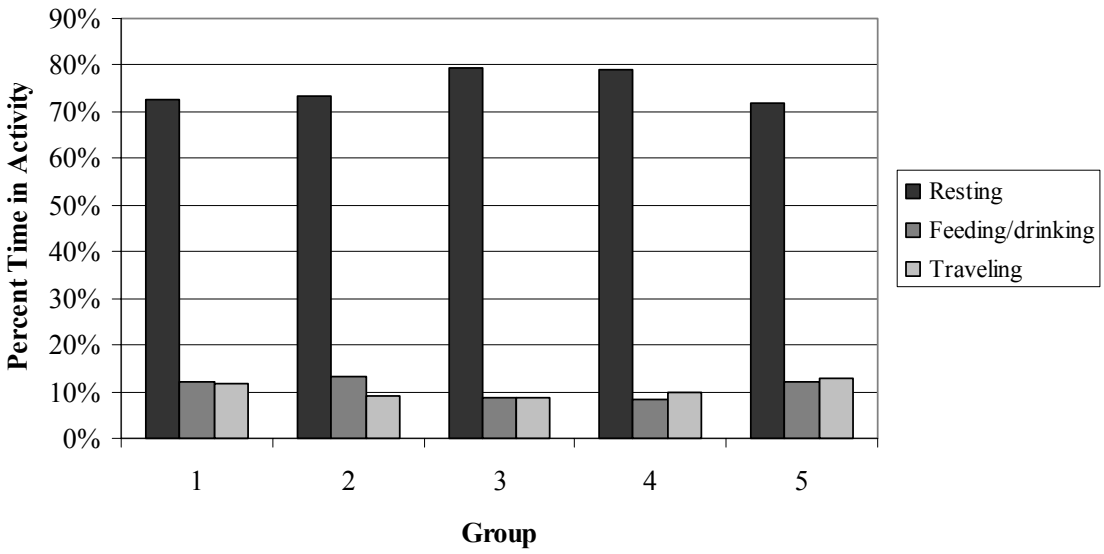


Figure 3.13. General time budget for each group. Groups 1 and 2 are located in Vatoharanana; groups 3, 4, and 5 are located in Talatakely. Group 5 more closely resembles groups in Vatoharanana than groups in Talatakely.

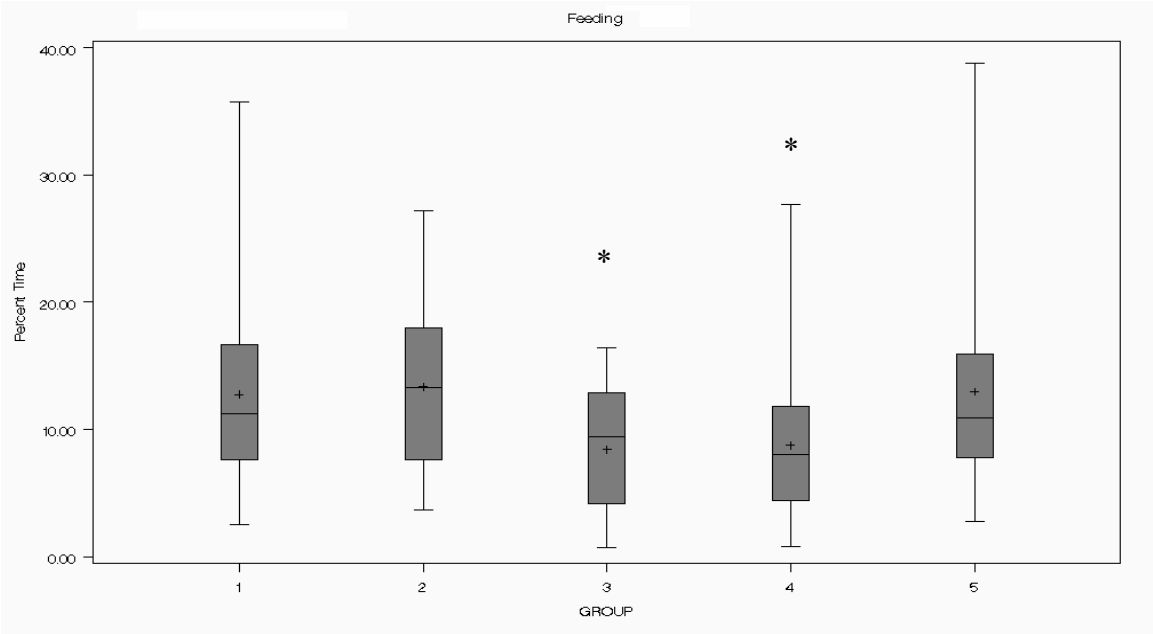


Figure 3.14. Mean relative amount of time spent feeding by each group throughout the study. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data. Groups 1 and 2 are located in Vatoharanana; Groups 3, 4, and 5 are located in Talatakely. Groups 3 and 4 spend significantly less time feeding than all groups except each other. Group 5 more closely resembles groups in Vatoharanana than groups in Talatakely.

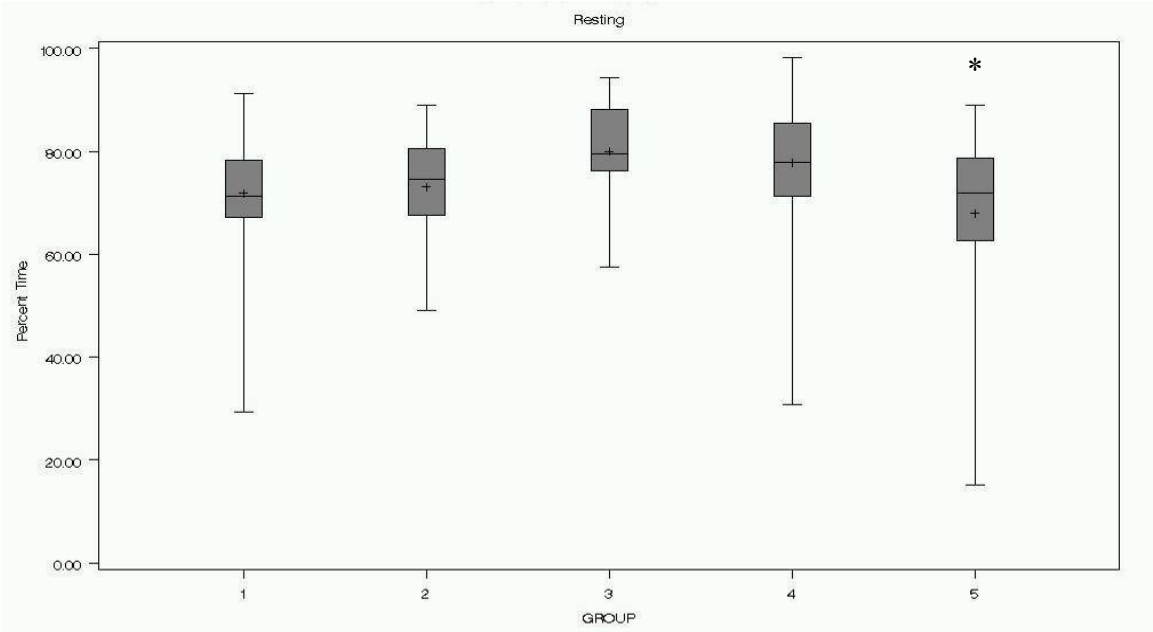


Figure 3.15. Mean relative amount of time spent resting by each group throughout the study. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data. Groups 1 and 2 are located in Vatoharanana; Groups 3, 4, and 5 are located in Talatakely. Group 5 is significantly different from all other groups ($p<.05$) and more closely resembles groups in Vatoharanana than groups in Talatakely. Excluding Group 5, all groups significantly differ only with groups located in a different site ($p<.01$).

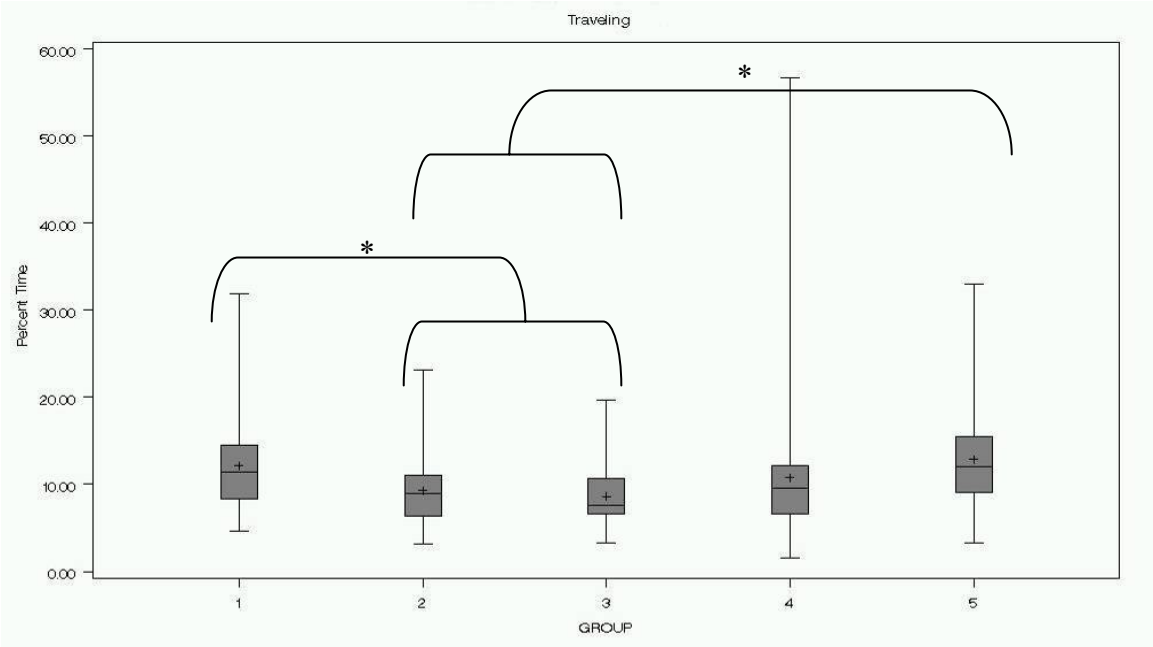
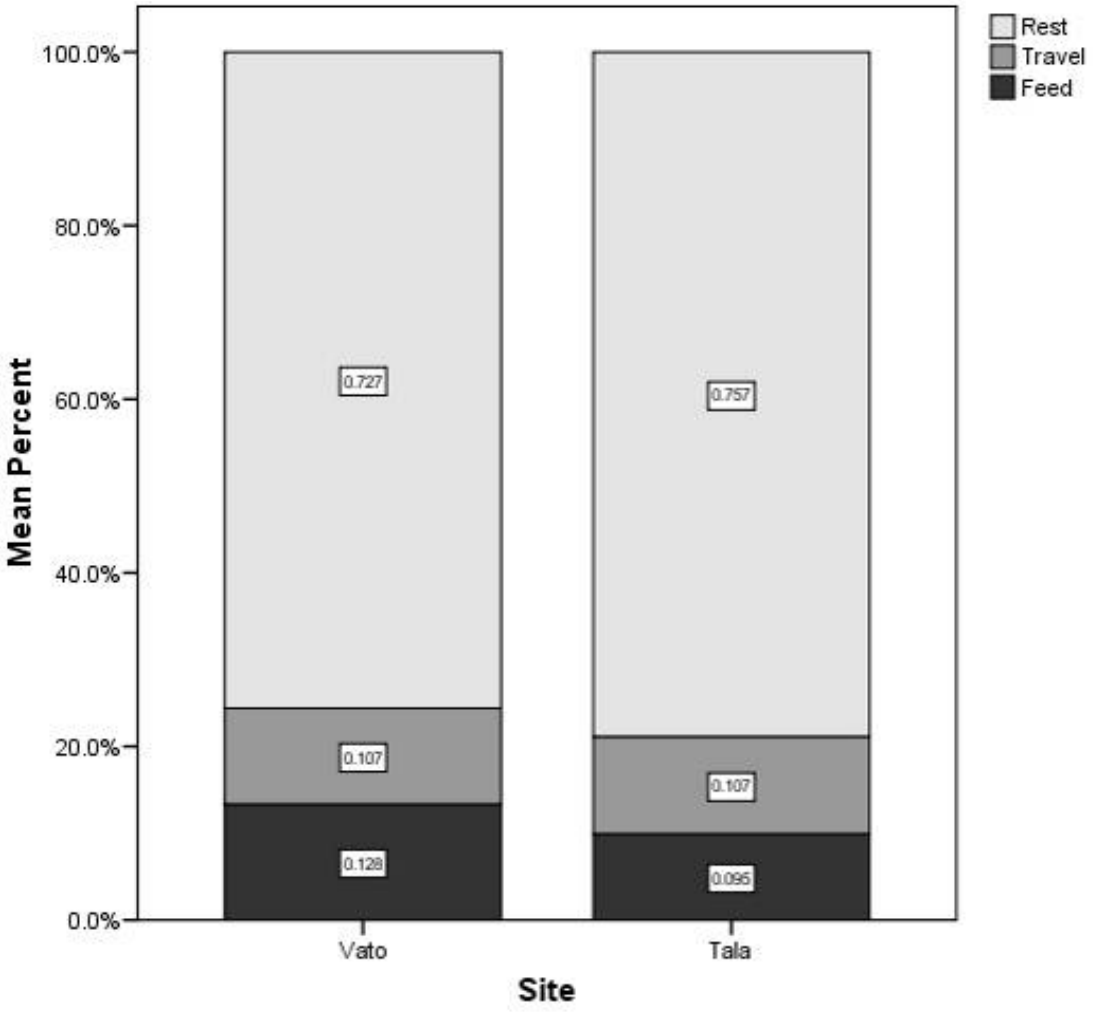


Figure 3.16. Mean relative amount of time spent traveling by each group throughout the study. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, and the whiskers outside the box enclose 5%-95% of the data. Groups 1 and 2 are located in Vatoharanana; Groups 3, 4, and 5 are located in Talatakely. Overall, group differences approached significance, $F(4,829)=2.28$, $p=0.0591$, while significant differences were present between certain pairs (see text). Group 1 ($p<.05$) and Group 5 ($p<.05$) traveled significantly more than Groups 2 and 3.

Table 3.7. Parameter estimates for feeding, resting, and traveling across groups. All groups are most similar to groups at the same site for each behavior except for Group 5. Only Group 5 is significantly different than groups located at the same site for time spent feeding and resting (in bold). All remaining significant differences are between groups located at different sites, except the amount of time spent traveling in Groups 1 and 2.

Behavior	Group	Standard Error	t-value	Numerator df	Denominator df	P-value	Same Site?
Feeding	1*2	1.45	-0.42	4	829	ns	Y
Feeding	1*3	1.64	2.64	4	829	**p<.01	N
Feeding	1*4	1.48	2.69	4	829	**p<.01	N
Feeding	1*5	1.62	-0.10	4	829	ns	N
Feeding	2*3	1.69	2.92	4	829	**p<.01	N
Feeding	2*4	1.54	2.98	4	829	**p<.01	N
Feeding	2*5	1.67	0.26	4	829	ns	N
Feeding	3*4	1.71	-0.20	4	829	ns	Y
Feeding	**3*5**	**1.84**	**-0.25**	**4**	**829**	***p<.05**	**Y**
Feeding	**4*5**	**1.70**	**-2.44**	**4**	**829**	***p<.05**	**Y**
Resting	1*2	1.45	-0.84	4	829	ns	Y
Resting	1*3	1.64	-4.99	4	829	***p<.001	N
Resting	1*4	1.46	-4.12	4	829	***p<.001	N
Resting	1*5	1.62	2.45	4	829	*p<.05	N
Resting	2*3	1.69	-4.11	4	829	***p<.001	N
Resting	2*4	1.52	-3.16	4	829	**p<.01	N
Resting	2*5	1.67	3.11	4	829	**p<.01	N
Resting	3*4	1.70	1.26	4	829	ns	Y
Resting	**3*5**	**1.84**	**6.61**	**4**	**829**	***p<.001**	**Y**
Resting	**4*5**	**1.68**	**5.95**	**4**	**829**	***p<.001**	**Y**
Traveling	1*2	1.45	1.98	4	829	*p<.05	Y
Traveling	1*3	1.64	2.17	4	829	*p<.05	N
Traveling	1*4	1.46	0.97	4	829	ns	N
Traveling	1*5	1.62	-0.39	4	829	ns	N
Traveling	2*3	1.69	0.40	4	829	ns	N
Traveling	2*4	1.52	-0.95	4	829	ns	N
Traveling	2*5	1.67	-2.10	4	829	*p<.05	N
Traveling	3*4	1.70	-1.25	4	829	ns	Y
Traveling	**3*5**	**1.84**	**-2.28**	**4**	**829**	***p<.05**	**Y**
Traveling	4*5	1.68	-1.23	4	829	ns	Y

(A) All groups


Rest
Travel
Feed
100.0%
80.0%
60.0%
40.0%
20.0%
0.0%
Mean Percent
0.727
0.107
0.128
0.757
0.107
0.096
Vato
Tala
Site

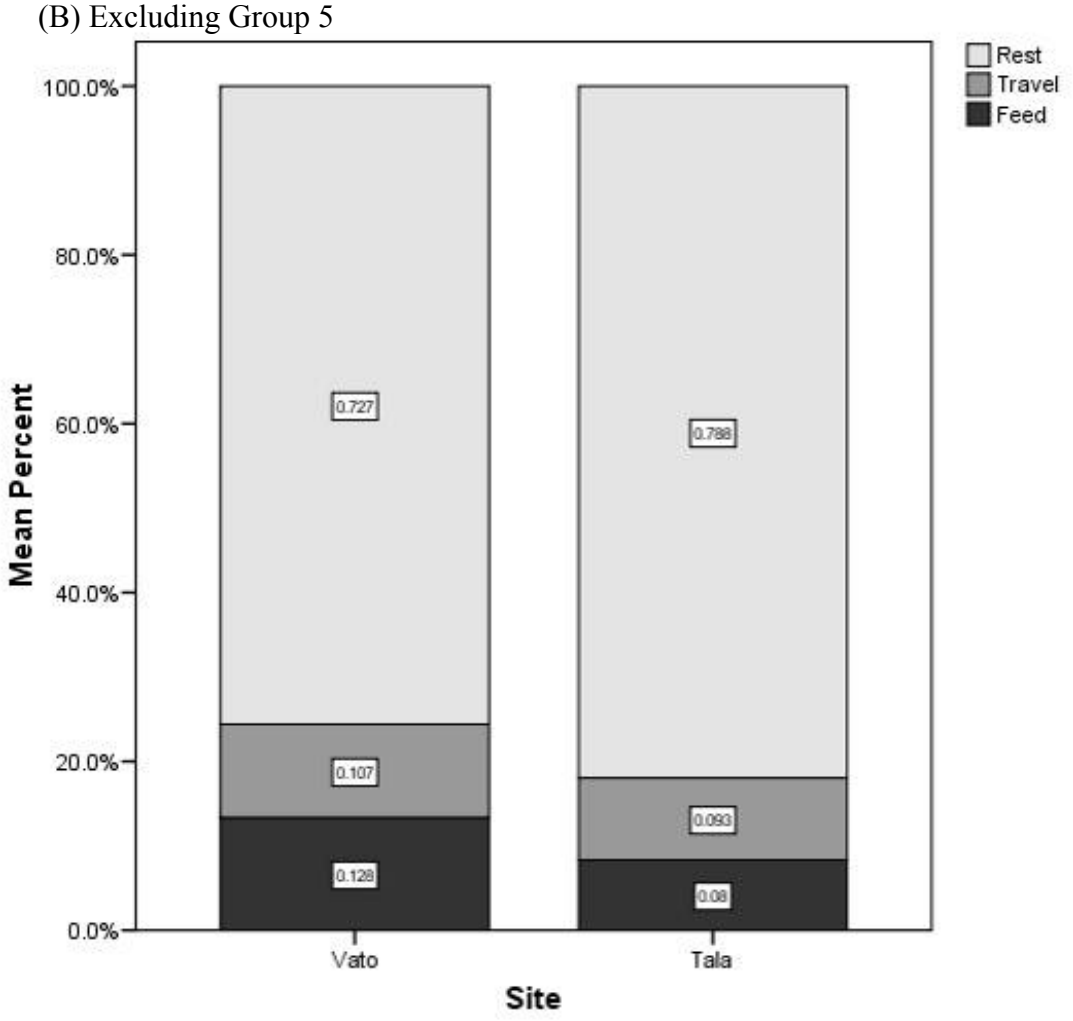


Figure 3.17. Overall time budget by site (A) for all groups, and (B) excluding group 5. Site differences are intensified when Group 5 is removed from the analysis.

Seasonal Time Budget

In a Mixed Model with all factors (temperature, rainfall, total fruit availability or ripe fruit availability, and site) fixed, proportion of time spent feeding and resting were significantly different between sites and in each dichotomous season except *total* fruit availability (Feeding: Table 3.8; Resting: Table 3.9). It should be noted that because of

the large overlap between temperature and rainfall seasons, additional models were run with site and each of these seasons separately. Results were similar for temperature seasons (Feeding: $F(1,184.001)=52.047$, $p<.001$; Resting: $F(1,266.965)=31.390$), but rainfall season was no longer significant (Feeding: $F(1,162.044)=3.766$, $p=.054$; Resting: $F(1,240.926)=0.591$, $p=.443$.

Overall, feeding was highest during the dry and warm seasons and resting was highest during the wet and cool seasons. Feeding was highest during both scarce seasons (total and ripe fruit), and resting was lowest during both scarce seasons, although feeding and resting were only significantly different between *ripe* fruit availability seasons. Feeding and resting appear to be inversely related in all seasons. Ripe fruit availability season was more biologically significant to *Eulemur rubriventer* than total fruit availability season.

Proportion of time spent traveling overall was significantly different between each climate season (rainfall and temperature), but not during either fruit availability season, nor between sites (Table 3.10). Furthermore, when individual seasonal models were run as above, traveling was not significant between either climate season (temperature: $F(1,196.432)=3.588$, $p=.06$; rainfall: $F(1,190.798)=2.519$, $p=.114$). This indicates that the amount of traveling may only be related to rainfall and temperature. Animals traveled more in the dry season and warm season in both models.

Table 3.8. Type III Tests of Fixed Effects for mixed model including all seasonal variables on percent time feeding. (A) Results from the first model incorporating Total Fruit Availability season. (B) Results from the second model substituting Ripe Fruit Availability season for Total Fruit Availability season.

(A) Feed Total Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	155.63	18.852	***p<.001
Rainfall	1	252.63	5.880	*p<.05
Temperature	1	242.07	50.946	***p<.001
Total Fruit	1	224.52	1.419	ns

(B) Feed Ripe Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	160.20	20.481	***p<.001
Rainfall	1	218.46	11.356	***p<.001
Temperature	1	226.94	57.232	***p<.001
Ripe Fruit	1	235.670	5.146	*p<.05

Table 3.9. Type III Tests of Fixed Effects for mixed model including all seasonal variables on time spent resting. (A) Results from the first model incorporating Total Fruit Availability season. (B) Results from the second model substituting Ripe Fruit Availability season for Total Fruit Availability season.

(A) Rest Total Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	249.647	6.924	$**p<.01$
Rainfall	1	315.651	12.240	$***p<.001$
Temperature	1	304.174	43.082	$***p<.001$
Total Fruit	1	300.139	.554	ns

(B) Rest Ripe Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	254.69	7.658	$**p<.01$
Rainfall	1	287.24	13.490	$***p<.001$
Temperature	1	293.96	41.251	$***p<.001$
Ripe Fruit	1	294.32	3.902	$*p<.05$

Table 3.10. Type III Tests of Fixed Effects for mixed model including all seasonal variables on time spent traveling. (A) Results from the first model incorporating Total Fruit Availability season. (B) Results from the second model substituting Ripe Fruit Availability season for Total Fruit Availability season.

(A) Travel Total Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	174.45	0.015	ns
Rainfall	1	252.75	12.191	***p<.001
Temperature	1	241.10	13.887	***p<.001
Total Fruit	1	232.10	0.278	ns

(B) Travel Ripe Fruit Season

Source	Numerator df	Denominator df	F	Significance
Site	1	179.78	0.047	ns
Rainfall	1	221.43	13.797	***p<.001
Temperature	1	228.95	12.629	***p<.001
Ripe Fruit	1	232.59	2.349	ns

Climate

Temperature Seasons

All Individuals: Using a Mixed Model for percent time feeding by week and temperature season, with temperature season fixed, the overall amount of time red-bellied lemurs devoted to feeding and resting was significantly different between cool and warm seasons ($F(1,181.159)=46.293$, $p<.001$; $F(1,261.483)=30.04$, $p<.001$, respectively) as predicted (Figure 3.18), though traveling did not differ across seasons, $F(1,197.995)=3.604$, $p=.059$. During the cool season, lemurs rested more and fed and

traveled less, as predicted. This pattern may be one that minimizes time and energy expenditure in the cool season. Table 3.12A summarizes cross-season trends.

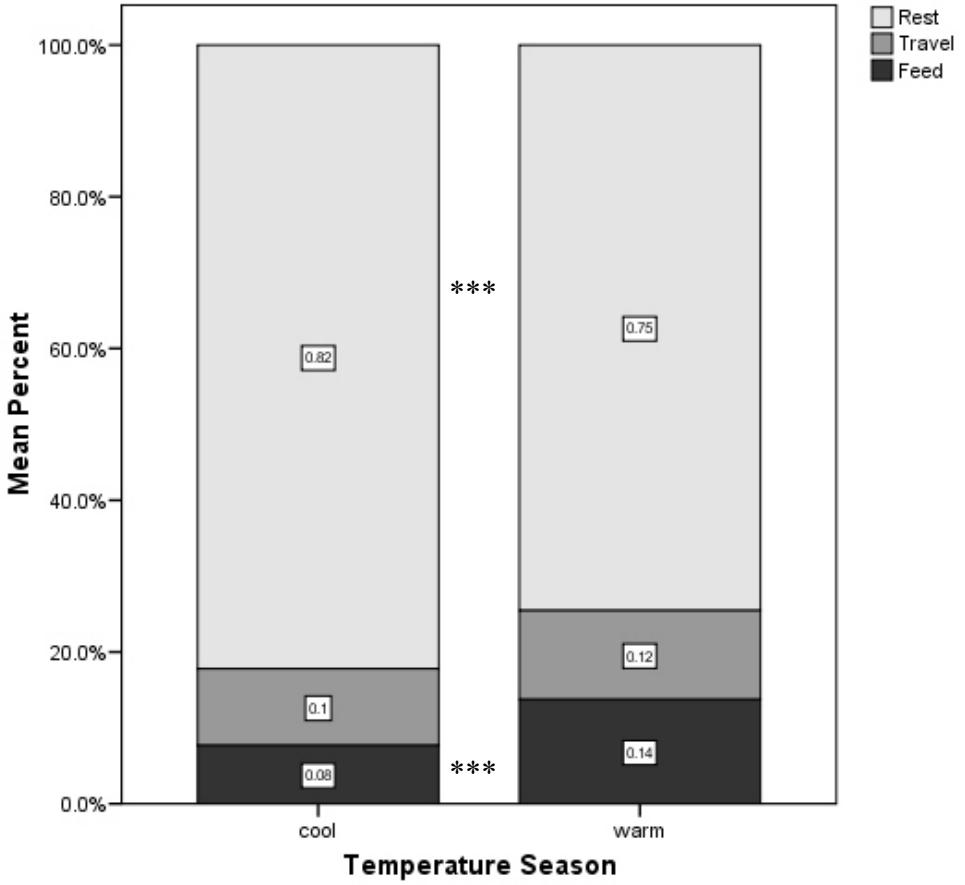


Figure 3.18. Time budget by temperature season. Time spent resting and traveling significantly differed across seasons, $p<.001$.

Sites: To determine if animals in each site responded to changes in climate seasons similarly, a mixed model was used with fixed factors temperature, site, and temperature by site. There was a significant interaction effect between site and temperature season on time spent feeding, $F(1,253.67)=12.315$, $p<.001$, where seasonal differences (more time feeding during the warm season) were stronger in Vatoharanana

(Figure 3.19). No interaction effects were found for resting, F(1,184.34)=1.668, ns, nor traveling, F(1,120.63)=3.064, ns.

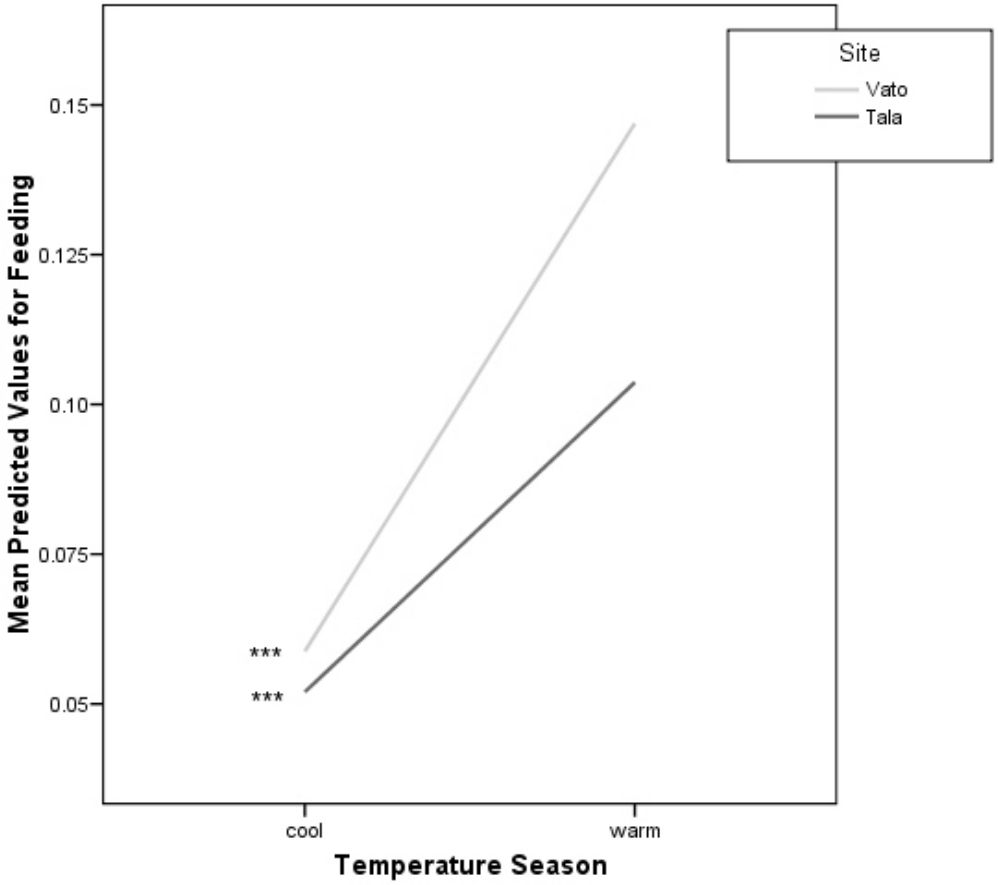


Figure 3.19. Interaction effects between site and temperature season on time spent feeding. Mean predicted values generated by the model represent differences in the strength of this relationship among sites, $p<.001$.

Groups: There were significant interaction effects between group and temperature season on the amount of time spent feeding, resting, and traveling ($F(4,179.54)=6.866$, $p<.001$; $F(4,123.94)=3.576$ $p<.01$; $F(4,116.27)=3.724$, $p<.001$, respectively). All groups fed less and rested more during the cool season. However, this relationship was not significant in Group 5 (Table 3.11AB). Traveling between seasons

differed among groups. Groups 4 and 5 were exceptional in that they traveled *more* during the cool season, while the remaining groups traveled *less* during the cool season. Since all groups experienced similar climates, these differences may be related to other factors such as microhabitat (Tecot, 2006), reproductive stage (not all groups gave birth synchronously) (Tecot and Overdorff, 2005), or territorial defense (of territories of variable sizes). However, visual inspection of predicted means found that this trend was particularly weak in Group 5 (Table 3.11C, Figure 3.20). As noted previously, Group 4's range was extensive, and relatively greater traveling during the cool season may be more closely related to resource distribution than climate.

Table 3.11. Univariate Tests of percent time (A) feeding, (B) resting, and (C) traveling in each group across temperature seasons. Although not all relationships were significant, all were in the same direction.

(A) Feeding

Group	Numerator df	Denominator df	F	Significance
1	1	63.86	56.08	***p<.001
2	1	64.37	172.75	***p<.001
3	1	57.28	39.81	***p<.001
4	1	71.49	25.58	***p<.001
5	1	84.36	4.76	ns

(B) Resting

Group	Numerator df	Denominator df	F	Significance
1	1	167.86	27.642	***p<.001
2	1	157.10	32.225	***p<.001
3	1	74.49	28.187	***p<.001
4	1	97.89	4.413	*p<.05
5	1	142.50	0.836	ns

(C) Traveling

Group	Numerator df	Denominator df	F	Significance
1	1	144.60	15.21	**p<.01
2	1	135.59	24.85	ns
3	1	89.64	7.79	**p<.01
4	1	85.04	0.08	ns
5	1	105.97	0.00	ns

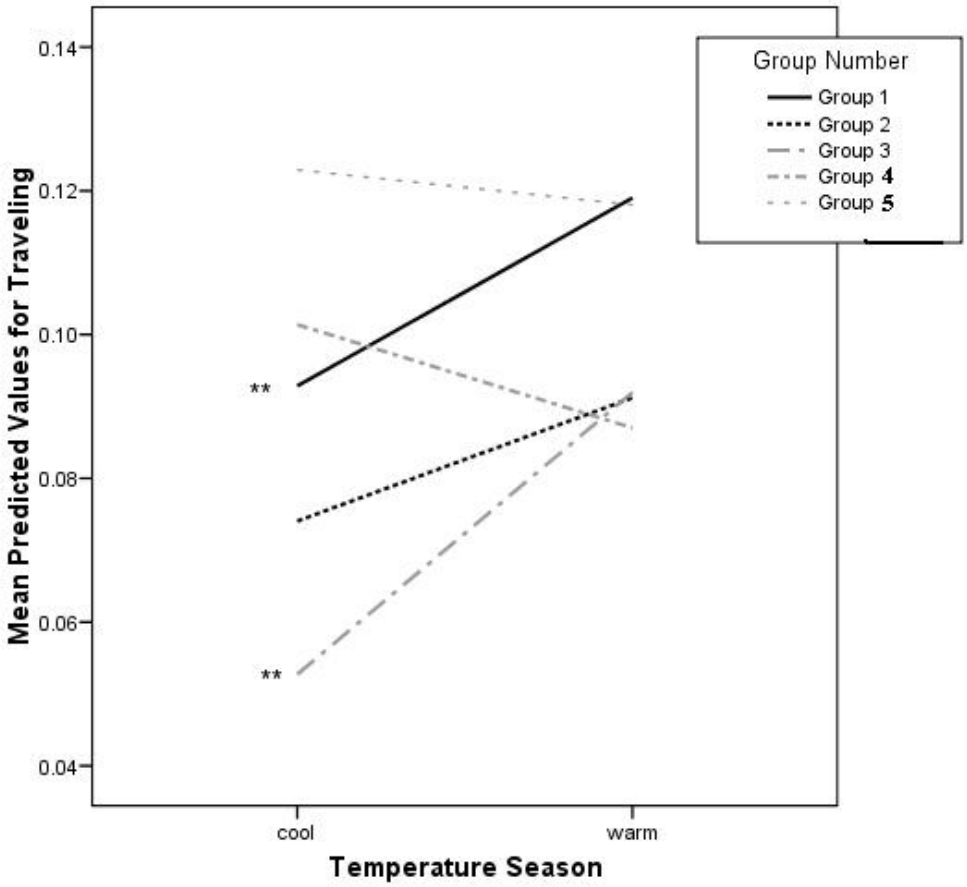


Figure 3.20. Interaction effects between group and temperature seasons on traveling. Mean predicted values generated by the model represent differences in the strength and directionality of this relationship among sites, $p<.001$. Groups 1-3 spent more time traveling during the warm season while Groups 4 and 5 spent more time traveling during the cool season.

Rainfall Seasons

All Individuals: In a Mixed Model predicting behavior by rainfall season and week, and rainfall season fixed, the overall amount of time devoted to feeding, resting, and traveling was not significantly different between dry and wet seasons ($F(1,163.518)=3.421$, $p=.066$; $F(1,237.072)=0.567$, $p=.452$; $F(1,192.913)=2.522$, $p=.114$, respectively) (Figure 3.21), as predicted. In partial support of predictions and patterns

observed in red ruffed lemurs, red-bellied lemurs fed less and rested and traveled more during the dry season. Less resting behavior in the wet season refutes the view that lemurs avoid thermal stress by huddling more at this time (but see below). Cool and dry season time budgets are similar, except that relative time spent traveling decreased in the cool season, while it increased in the dry season. Table 3.12B summarizes cross-season trends.

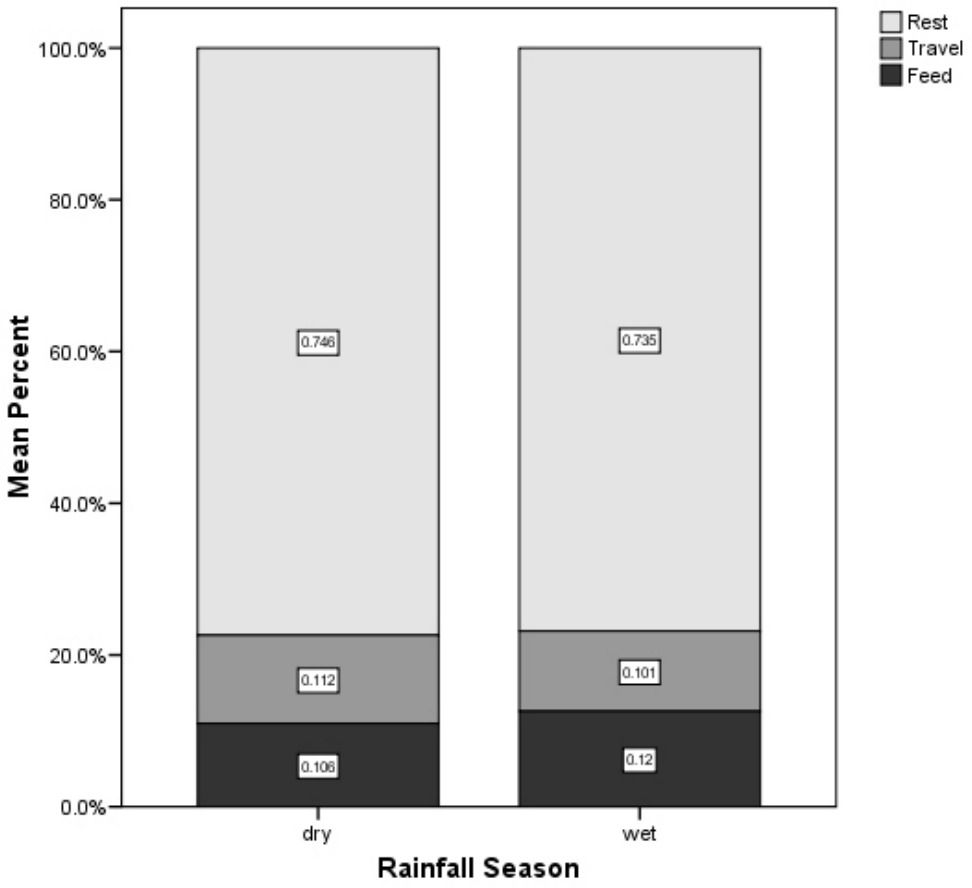


Figure 3.21. Time budget by rainfall season. Time spent performing each behavior did not significantly differ across seasons.

Table 3.12. Cross-season trends in time devoted to feeding, resting, and traveling for all animals combined. 'High' and 'low' indicate the seasons in which more or less time, respectively, was devoted to the noted behavior. All differences between temperature (A) and rainfall (B) seasons are significant at $p<.001$. For feeding and resting, differences between cool and warm seasons are similar to differences between dry and wet seasons, respectively.

(A) Temperature seasons

Feed	**Low**	**High**
Rest	**High**	**Low**
Travel	Low	High

(B) Rainfall seasons

Feed	**Low**	**High**
Rest	**High**	**Low**
Travel	High	Low

Sites: In a mixed model with fixed factors rainfall, site, and rainfall by site, there was an interaction effect between site and rainfall season on the amount of time spent resting, $F(1,177.57)=4.482$, $p<.05$. Resting in Talatakely was greater during the dry season and lower during the wet season, and resting in Vatoharanana was lower during the dry season and greater in the wet season (Figure 3.22). Neither of these differences was significant, but caution should be used when interpreting the overall significant trend of increased resting during the dry season, since clearly factors other than rainfall are contributing to this pattern. Differences between sites are discussed below.

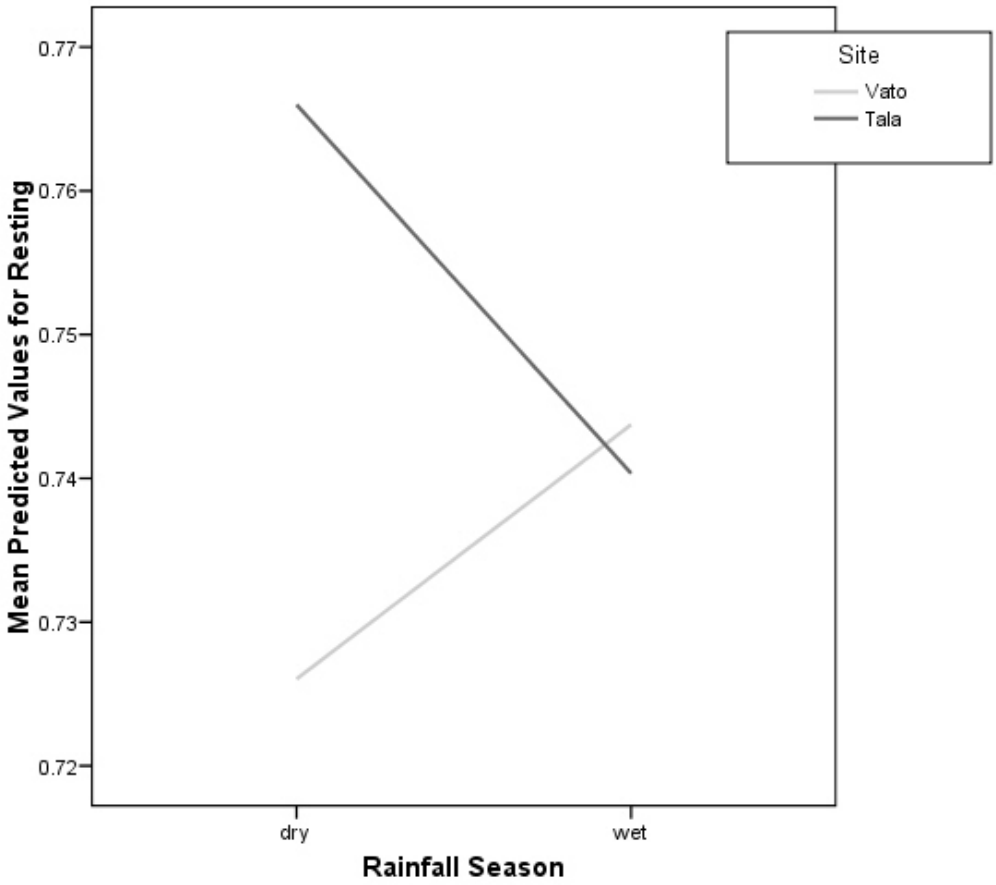
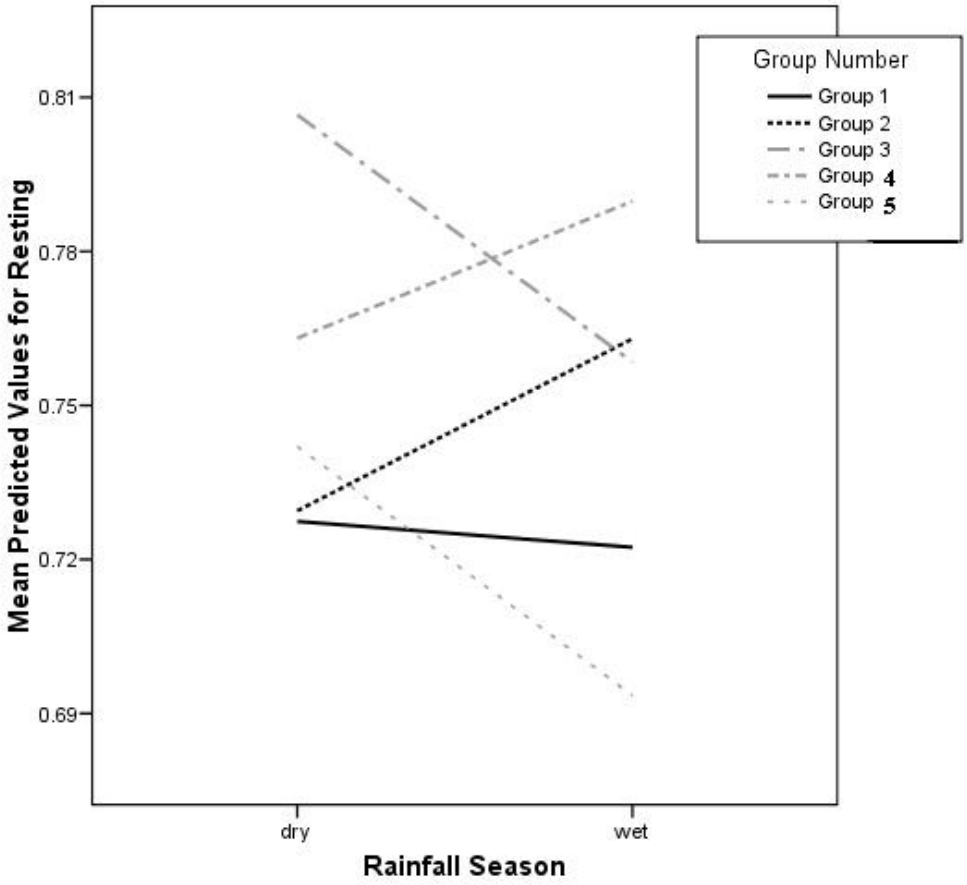


Figure 3.22. Interaction effects between site and rainfall season on time spent resting. Mean predicted values generated by the model represent differences in the strength and directionality of this relationship among sites, $p<.05$.

Groups: There was a significant interaction effect between group and rainfall season on the amount of time spent resting ($F(4,183.99)=2.666$, $p<.05$). Although groups showed different trends from one another (either increasing or decreasing time spent resting), there were no significant differences in the amount of time resting across rainfall seasons within any group (Table 3.13B, Figure 3.23A). Group 3 significantly differed from all other groups during the dry season except Group 4, where p=0.051.

While there was not an interaction effect between group and rainfall season on the amount of time traveling, F(4,143.54)=0.960, ns, the effect of group was interesting. Contrary to the overall trend in traveling, Groups 3 and 5 spent more time traveling during the *wet* season, although visual inspection of predicted means found that this trend was particularly weak in group 5 (Figure 3.23B). No differences were significant (Table 3.10B). Again, since all groups experienced similar climates, these differences may be related to other factors such as microhabitat, reproductive stage, or territorial defense. The possibility remains that the effect of rainfall on red-bellied lemurs is relatively weak.

(A) Resting



(B) Traveling

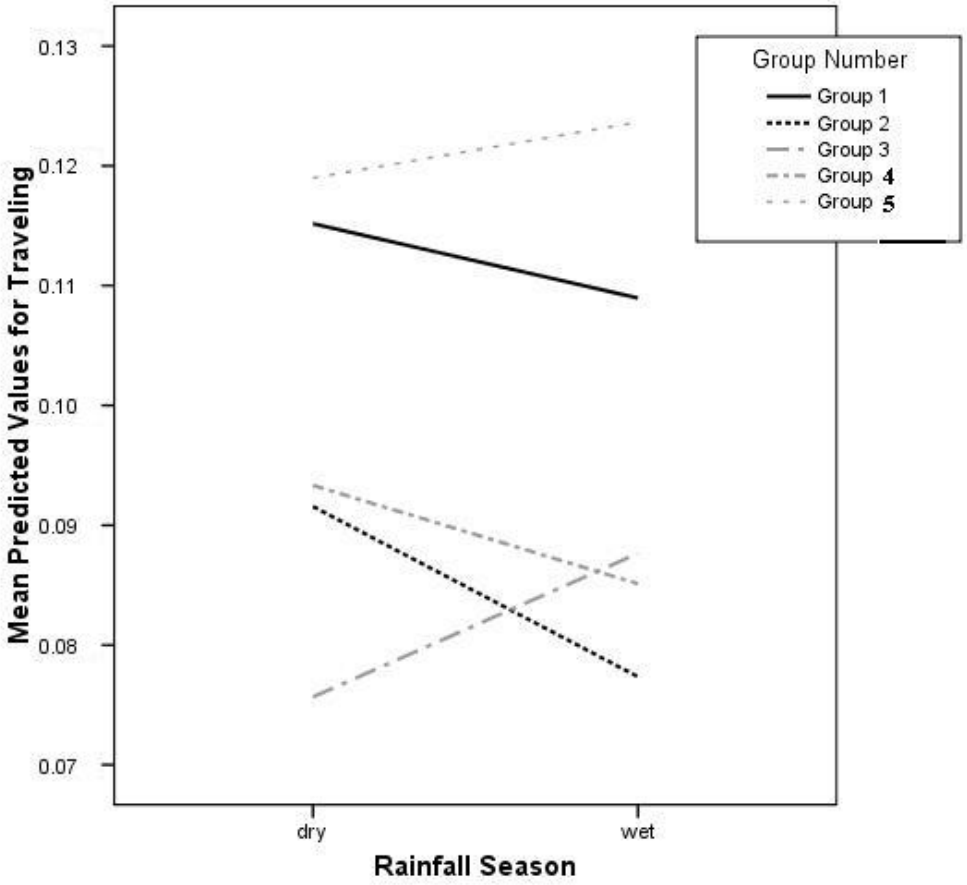


Figure 3.23. Interaction effects between group and rainfall season on feeding, resting, and traveling. Mean predicted values generated by the model indicate cross-season trends. (A) Groups 1, 3, and 5 spent more time resting in the dry season, while groups 2 and 4 spent more time resting in the wet season. (B) Groups 1, 2, and 4 spent more time traveling during the dry season, while groups 3 and 5 spent more time traveling during the wet season. No interaction group differences were significant.

Table 3.13. Univariate Tests of percent time (A) feeding, (B) resting, and (C) traveling in each group across rainfall seasons. Although not all relationships were significant, all displayed the same trend with the exception of Group 5 (resting and traveling).

(A) Feeding

Group	Numerator df	Denominator df	F	Significance
1	1	195.24	6.662	*p<.05
2	1	201.65	2.324	ns
3	1	177.69	8.495	*p<.01
4	1	176.16	0.001	ns
5	1	194.59	1.201	ns

(B) Resting

Group	Numerator df	Denominator df	F	Significance
1	1	244.527	0.057	ns
2	1	206.254	2.809	ns
3	1	124.540	3.327	ns
4	1	143.297	1.053	ns
5	1	186.485	3.514	ns

(C) Traveling

Group	Numerator df	Denominator df	F	Significance
1	1	98.029	.455	ns
2	1	80.856	2.645	ns
3	1	151.017	.996	ns
4	1	132.417	.506	ns
5	1	221.384	.151	ns

Food Availability

To determine if there was an effect of food availability upon time budget, the amount of time devoted to feeding, resting, and traveling was compared during food abundance and food scarcity seasons. As noted above, food availability seasons were determined in two ways: by total fruit availability, and by ripe fruit availability. Total fruit availability proved to be less predictive of behavioral changes, so only ripe fruit availability seasons are reported here.

Ripe fruit availability

All Individuals: Time spent feeding, resting, and traveling were significantly different across ripe fruit seasons. Time spent feeding was significantly greater during ripe fruit scarcity, $F(1,281.88)=56.152$, $p<.001$. Time spent resting was significantly greater during ripe fruit abundance, $F(1,186.96)=23.275$, $p<.001$. Time spent traveling was significantly greater during ripe fruit scarcity, $F(1,226.26)=12.836$, $p<.001$ (Figure 3.24). See Table 3.14A for overall seasonal trends for each behavior.

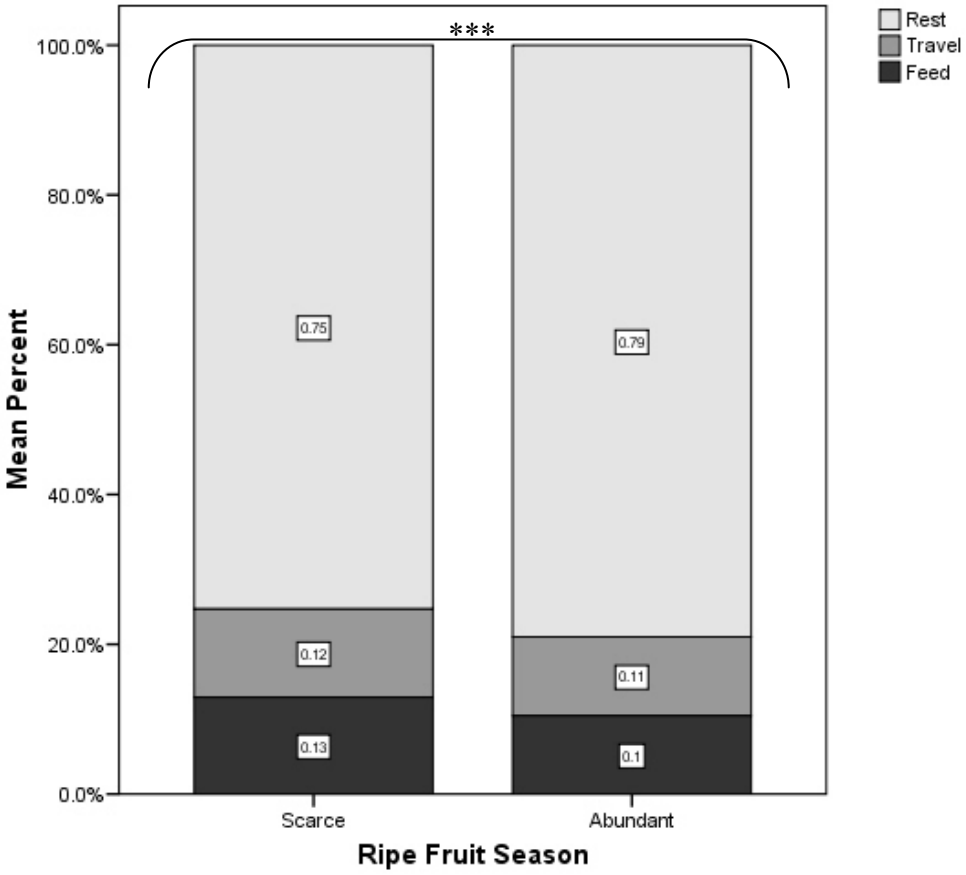


Figure 3.24. Time budgets for scarce and abundant ripe fruit seasons, $p<.001$. Note that the graph represents percentages for all individuals combined, while the MIXED model considered behavioral changes within each individual. Thus, the graphical representation of seasonal differences underestimates cross-season trends.

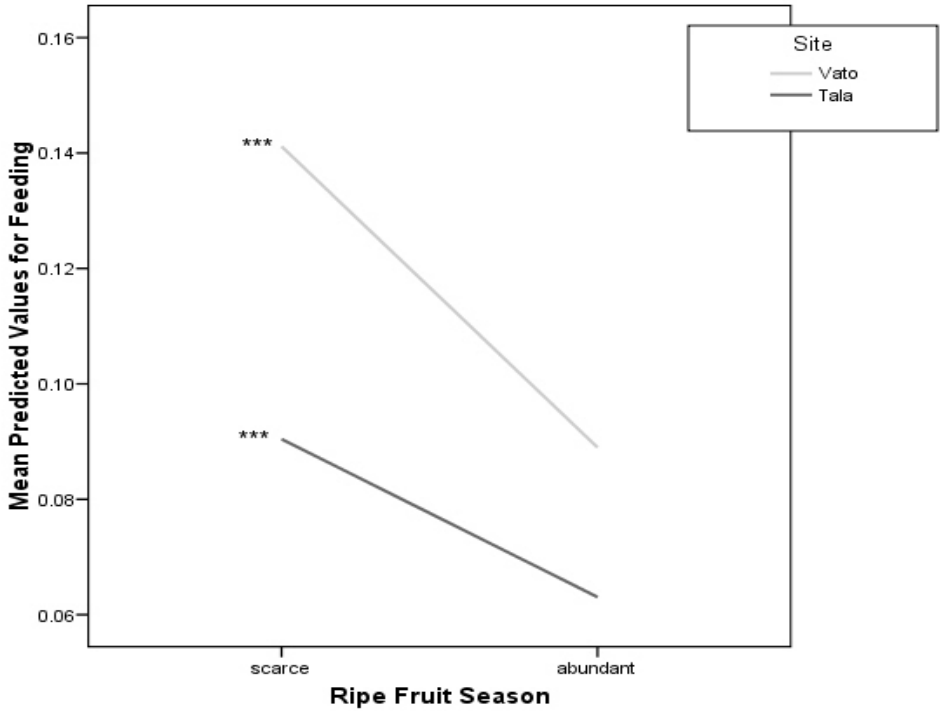
Sites: Time spent feeding, resting, and traveling across ripe fruit seasons followed the same trend in each site. However, all seasonal shifts in time budget were stronger in Vatoharanana, the undisturbed site. Time spent feeding was significantly greater during ripe fruit scarcity, $F(1,255.32)=52.021$, $p<.001$, although this relationship (significantly more feeding in the scarce season) was stronger in Vatoharanana, $F(1,216.35)=46.305$, $p<.001$, than in Talatakely, $F(1,249.79)=11.922$, $p<.001$ (Figure 3.25A).

Time spent resting was significantly lower during ripe fruit scarcity, $F(1,181.04)=27.063$, $p<.001$, but this relationship (significantly less resting in the scarce season) was only significant in Vatoharanana, $F(1,196.89)=31.421$, $p<.001$, and not in Talatakely, $F(1,158.26)=3.226$, $p=0.074$ (Figure 3.25B).

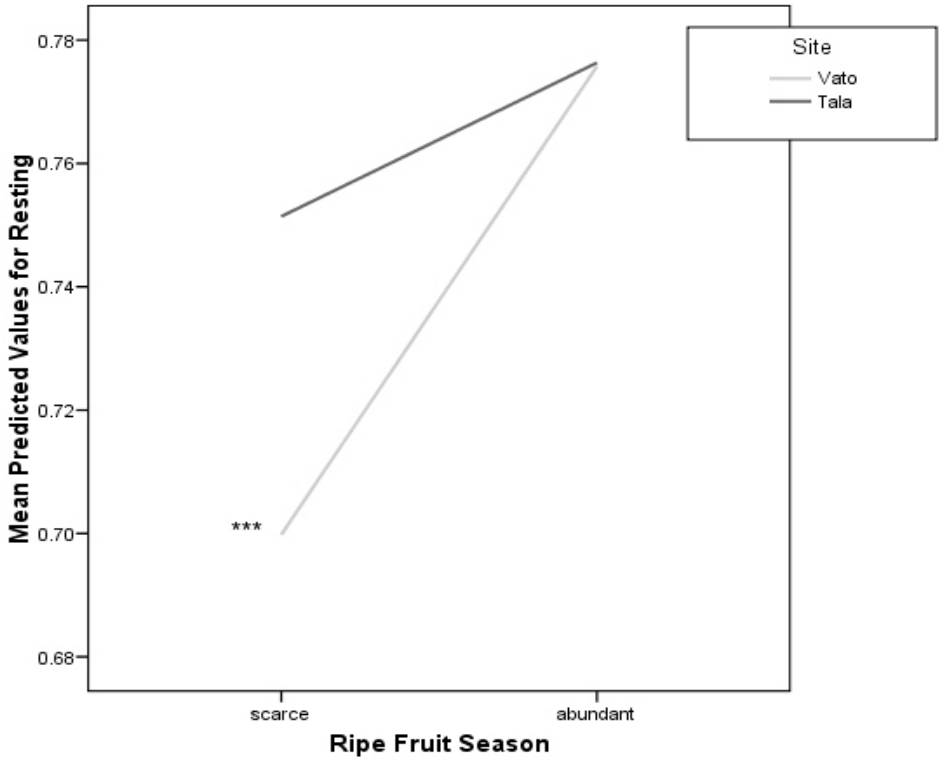
Time spent traveling was significantly greater during ripe fruit scarcity, $F(1,223.15)=16.287$, $p<.001$, yet this relationship (significantly more traveling in the scarce season) was only significant in Vatoharanana, $F(1,248.78)=31.128$, $p<.001$, but not in Talatakely, $F(1,192.15)=0.035$, $p=0.851$ (Figure 3.25C).

See Table 3.14B for seasonal trends in each behavior in each site.

(A) Feeding



(B) Resting



(C) Traveling

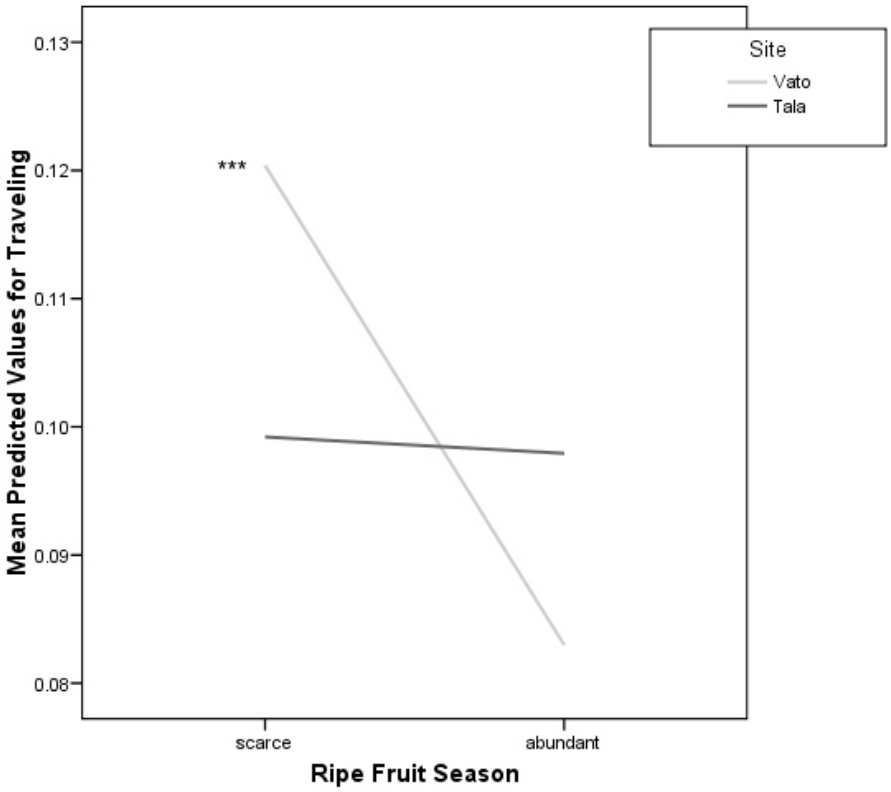


Figure 3.25. Plot of predicted means for feeding across ripe fruit availability seasons by site. Mean predicted values are based on the model. (A) There was a stronger relationship between feeding and ripe fruit season in Vatoharanana, although this relationship was very strong in both sites. (B) The relationship between resting and ripe fruit season was significant in Vatoharanana only. (C) The relationship between traveling and ripe fruit season was strong in Talatakely.

Groups: Group comparisons highlighted the weak relationships between feeding, resting, and traveling between seasons in Group 4, and more generally between seasons in Talatakely groups. While all groups in the study spent more time feeding during the scarce season, there was a significant effect of group on time spent feeding across ripe fruit seasons, $F(4,223.01)=3.082$, $p<.05$, where differences were significant only in

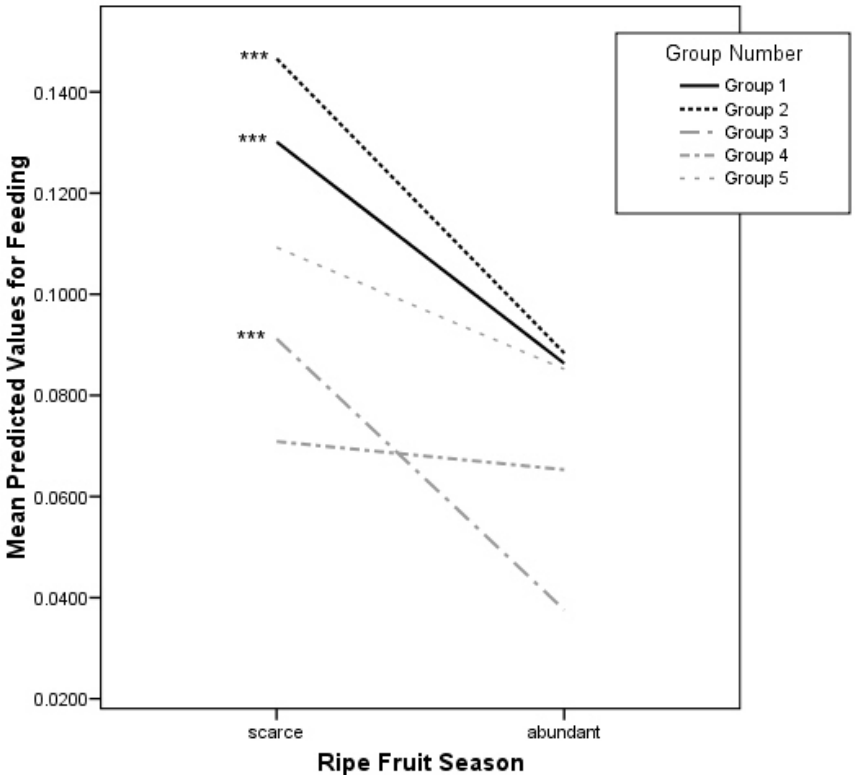
Groups 1-3 (p<.001), and this relationship was particularly weak in Group 4 (Figure 3.26A).

All groups spent more time resting during the abundant season, although there was a significant effect of group on time spent resting across ripe fruit seasons, F(4,189.87)=2.418, p=0.05. Differences were significant only in Groups 1-3 (p<.01), and this relationship was particularly week in Group 4 (Figure 3.26B).

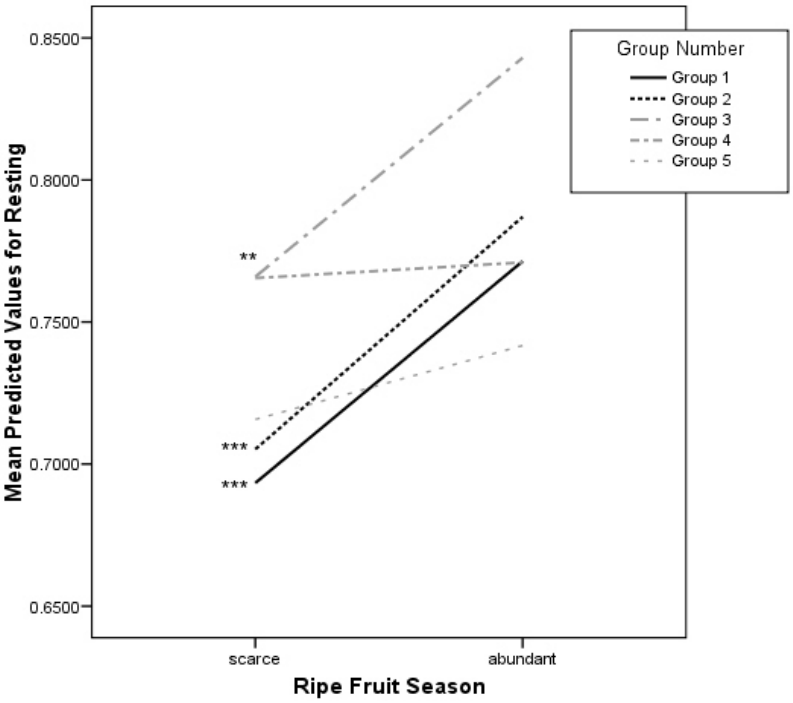
There was a significant effect of group on time spent traveling across ripe fruit seasons, F(4,185.44)=3.752, p<.01. All groups spent more time traveling in the scarce season except Group 4. Differences were significant in only Groups 1 and 2 (p<.001) (Figure 3.26C).

See Table 3.14C for seasonal trends in each behavior in each group.

(A) Feeding



(B) Resting



(C) Traveling

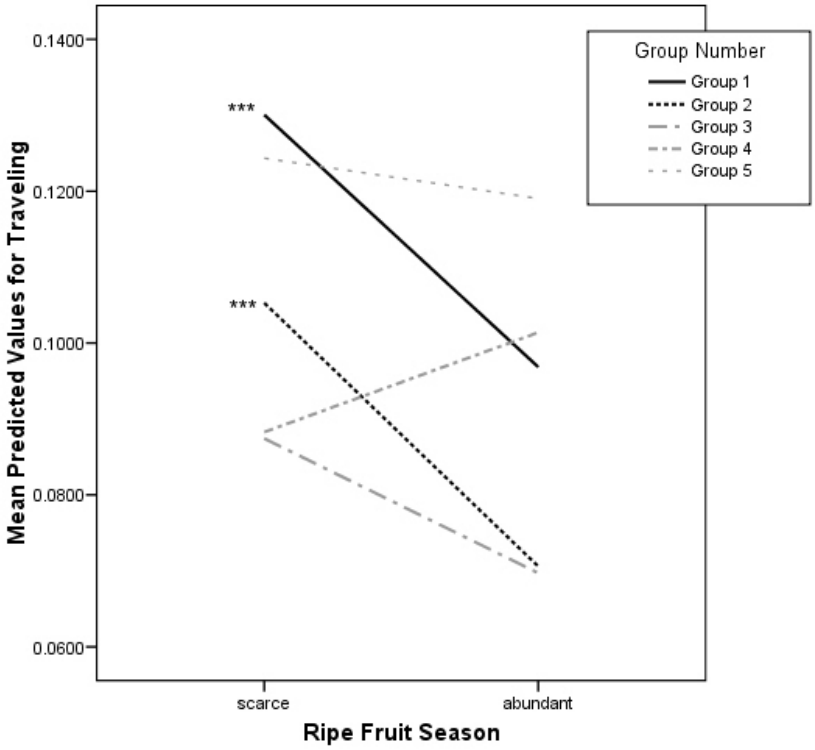


Figure 3.26. Feeding, resting, and traveling in scarce and abundant ripe fruit seasons, by group. (A) All groups spent more time feeding during the scarce season. (B) All groups spent more time resting during the abundant season. (C) Groups 1-3 and 5 spent more time traveling during the scarce season, while group 4 spent more time traveling during the abundant season. Asterisks denote seasonal differences within groups.

Table 3.14. Ripe fruit availability seasonal patterns in feeding, resting, and traveling. Results of tests based on the linearly independent pairwise comparisons among the estimated marginal means for feeding, resting, and traveling between ripe fruit availability seasons (A) overall, (B) by group, and (C) by site. 'High Season' reports the season in which time spent performing each behavior was highest. For instance, 'Scarce Season High' reports all groups or sites in which the most time spent performing any given behavior was during the scarce season.

(A) Overall

Behavior	High Season
Feeding	Ripe fruit scarcity***
Resting	Ripe fruit abundance***
Traveling	Ripe fruit scarcity***

(B) Groups

Behavior	Scarce Season High	Abundant Season High
Feeding	All Groups (1-3***, 4-5 ns)	
Resting		All Groups (1-2***, 3**, 4-5 ns)
Traveling	Groups 1, 2, 3, 5 (1-2***, 3-5 ns)	Group 4 (4 ns)

(C) Sites

Behavior	Scarce Season High	Abundant Season High
Feeding	Tala, Vato	
Resting		Tala, Vato
Traveling	Tala, Vato	

Seasonal Habitat Comparisons

Climate

Sites were compared with each other within each climate season for differences in feeding, resting, and traveling. In a mixed model with fixed factors site, temperature season, rainfall season, temperature season by site, and rainfall season by site, most of the predictions concerning differences between sites were unsupported. Talatakely groups were predicted to spend significantly more time feeding and resting and less time traveling than Vatoharanana groups. Vatoharanana groups spent more time feeding than Talatakely groups in all seasons, more time resting in cool and wet seasons, and more time traveling in warm and dry seasons.

Vatoharanana groups fed *significantly more* than Talatakely groups during the warm and dry seasons. Although Vatoharanana groups also fed more than Talatakely groups during the cool and wet seasons, these differences were not significant (Table 3.15A, Figure 3.27). In support of predictions, Talatakely groups rested significantly more in the warm and dry seasons and, contrary to predictions but not significant, less in the cool and wet seasons than Vatoharanana groups (Table 3.15B, Figure 3.28). Also in support of predictions, Talatakely groups traveled significantly less in the warm season and, contrary to predictions, significantly more in the cool and wet seasons than Vatoharanana groups (Table 3.15C, Figure 3.29). Talatakely groups did travel less than Vatoharanana groups in the dry season, although this only approached statistical significance, $F(1,102.02)=3.89$, $p=0.051$. Rather than more feeding and resting in the secondary forest, more feeding occurred consistently in the primary forest, and resting and traveling varied depending upon climate season.

Table 3.15. Univariate tests of the effect of site on seasonal time budget. Each F tests the simple effects of site within each level combination of the other effects shown. These tests are based on the linearly independent pairwise comparisons among the estimated marginal means for (A) feeding, (B) resting, and (C) traveling. Data are presented for temperature and rainfall seasons. 'High Site' reports the site in which the proportion of time spent performing each behavior was highest.

(A) Feeding

Cool	1	213.19	0.09	ns	Vato
Warm	1	142.84	36.99	***p<.001	Vato

Dry	1	116.82	20.86	***p<.001	Vato
Wet	1	202.48	0.88	ns	Vato

(B) Resting

Cool	1	218.24	1.55	ns	Vato
Warm	1	150.49	7.61	**p<.01	Tala

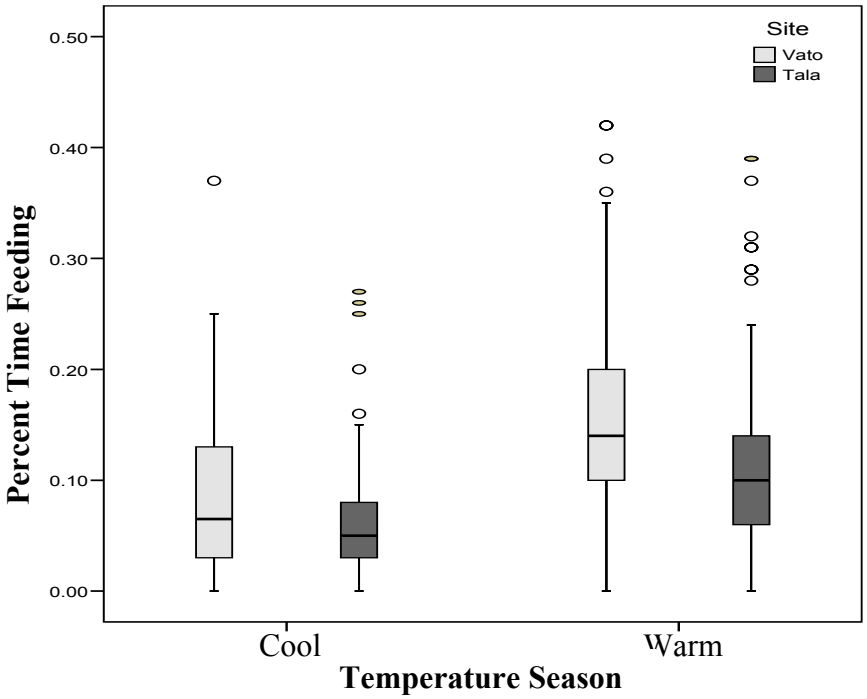
Dry	1	145.91	10.50	***p<.001	Tala
Wet	1	249.51	2.41	ns	Vato

(C) Traveling

Cool	1	127.68	7.99	**p<.01	Tala
Warm	1	105.94	7.19	**p<.01	Vato

Dry	1	102.02	3.89	ns	Vato
Wet	1	229.79	6.70	**p<.01	Tala

(A) Temperature



(B) Rainfall

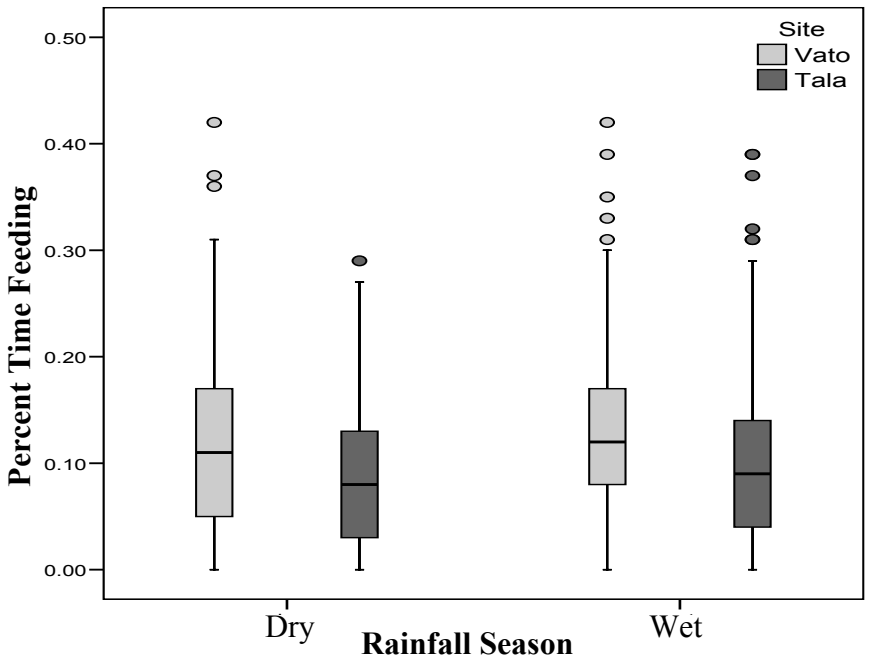
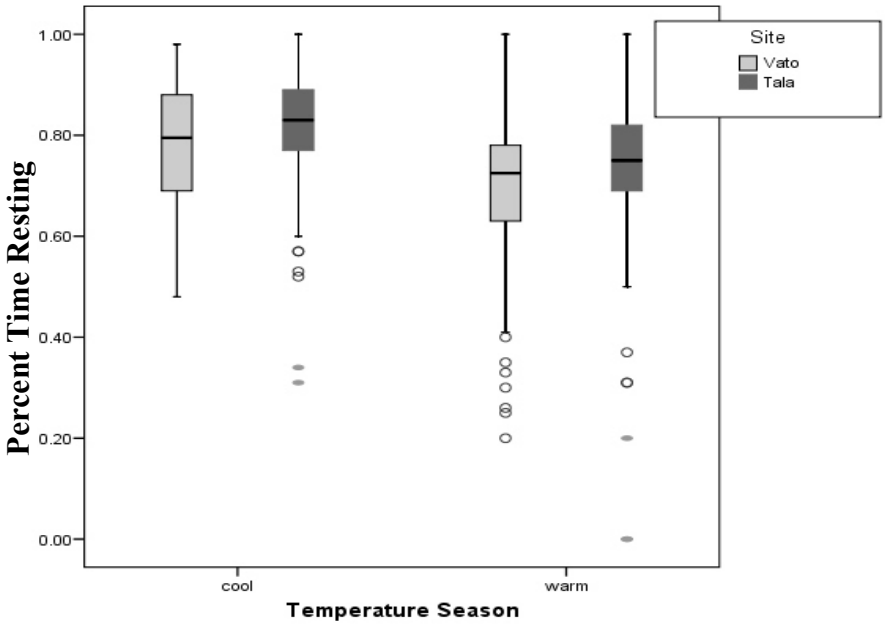


Figure 3.27. Boxplot of feeding among sites during (A) temperature (cool and warm) and (B) rainfall (dry and wet) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and filled circles represent outliers.

(A) Temperature



(B) Rainfall

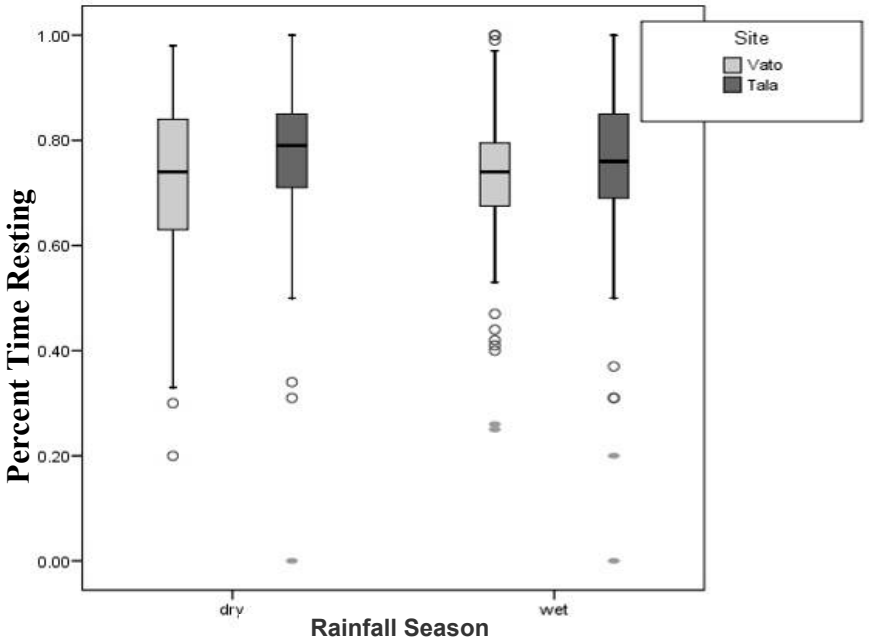
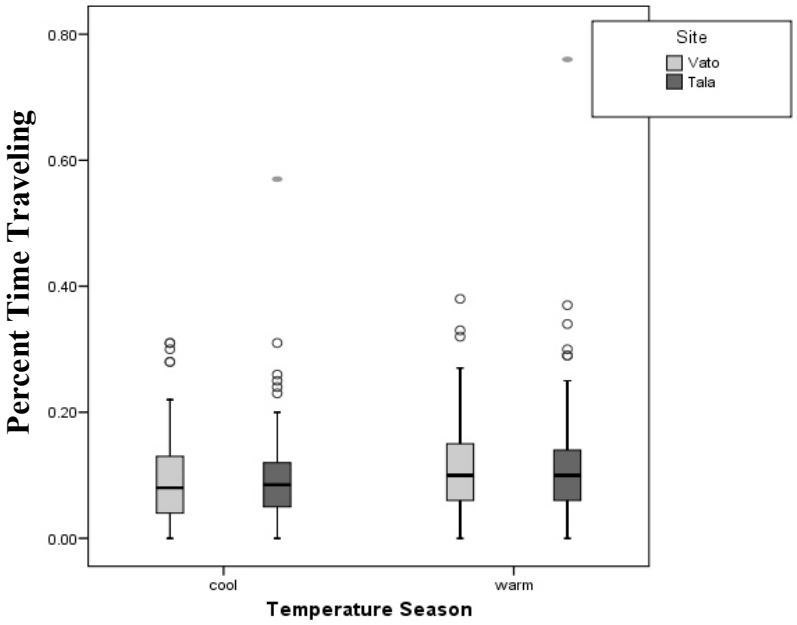


Figure 3.28. Site comparisons of resting during (A) temperature (cool and warm) and (B) rainfall (dry and wet) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and filled circles represent outliers.

(A) Temperature



(B) Rainfall

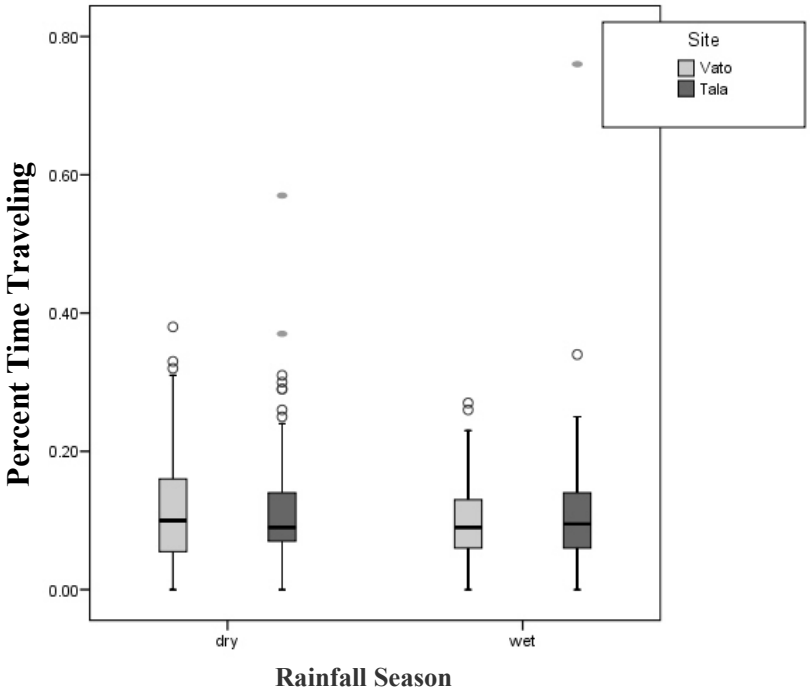


Figure 3.29. Site comparisons of traveling during (A) temperature (cool and warm) and (B) rainfall (dry and wet) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and filled circles represent outliers.

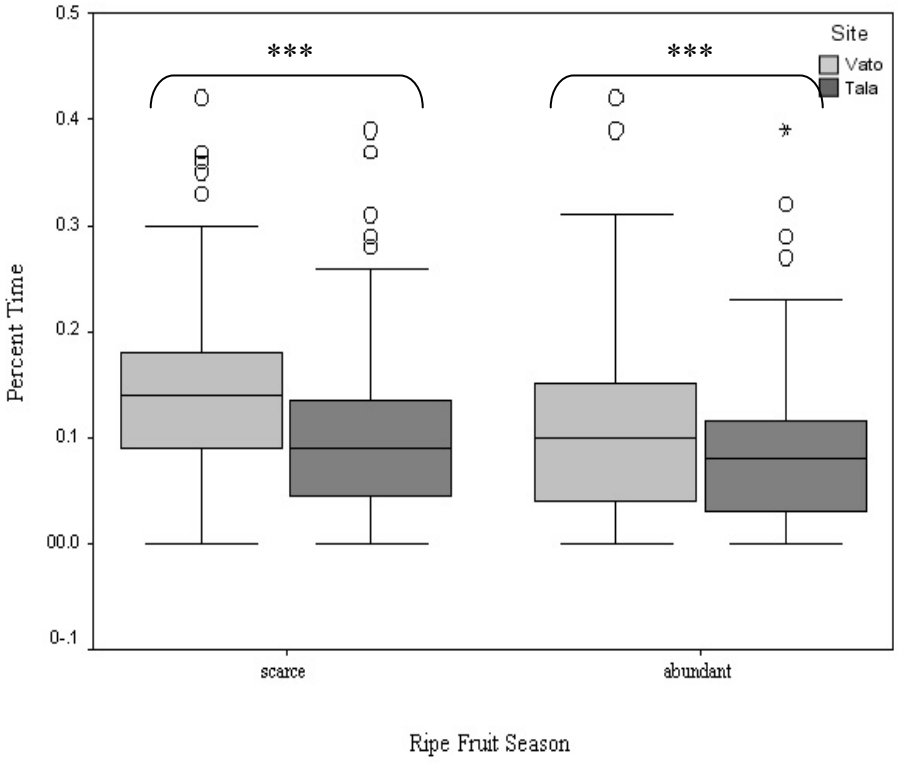
Fruit Availability

Feeding in Vatoharanana was significantly greater than feeding in Talatakely during both the scarce, $F(1,189.45)=35.698$, $p<.001$, and abundant, $F(1,153.81)=13.554$, $p<.001$, seasons. As predicted, time spent resting in Talatakely was significantly greater than resting in Vatoharanana during the scarce season, $F(1,48.68)=16.556$, $p<.001$, but there was no difference in the proportion of time spent resting between sites during the abundant season, $F(1,207.348)=0.001$, $p=0.969$. Time spent traveling in Vatoharanana was significantly greater than traveling in Talatakely during the scarce season, $F(1,130.28)=9.965$, $p<.01$, and, as predicted, significantly less during the abundant season, $F(1,113.688)=4.759$, $p<.05$. See Table 3.16 for site differences within each season.

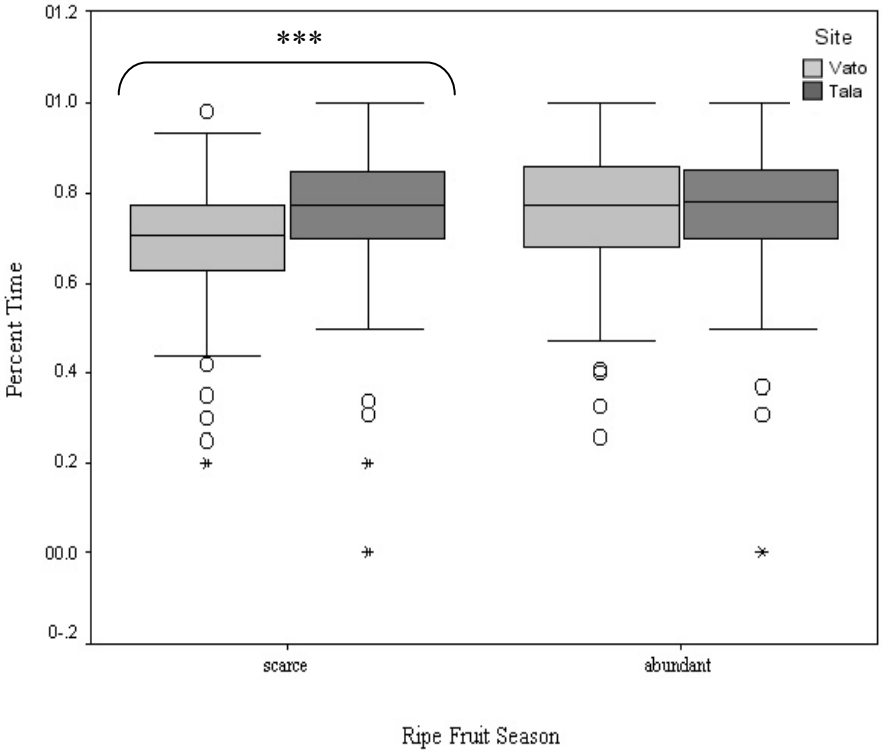
Table 3.16. Ripe fruit availability seasonal patterns in feeding, resting, and traveling between sites within each season. These tests are based on the linearly independent pairwise comparisons among the estimated marginal means for feeding, resting, and traveling between sites in Ripe Fruit Scarce and Ripe Fruit Abundant seasons. 'High' season reports the season in which time spent performing each behavior was highest. For instance, 'Scarce Season High' reports the site in which more time was spent performing the listed behaviors during the scarce season.

Behavior	Scarce Season High	Abundant Season High
Feeding	Vato***	Vato***
Resting	Tala***	ND
Traveling	Vato**	Tala*

(A) Feeding



(B) Resting



(C) Traveling

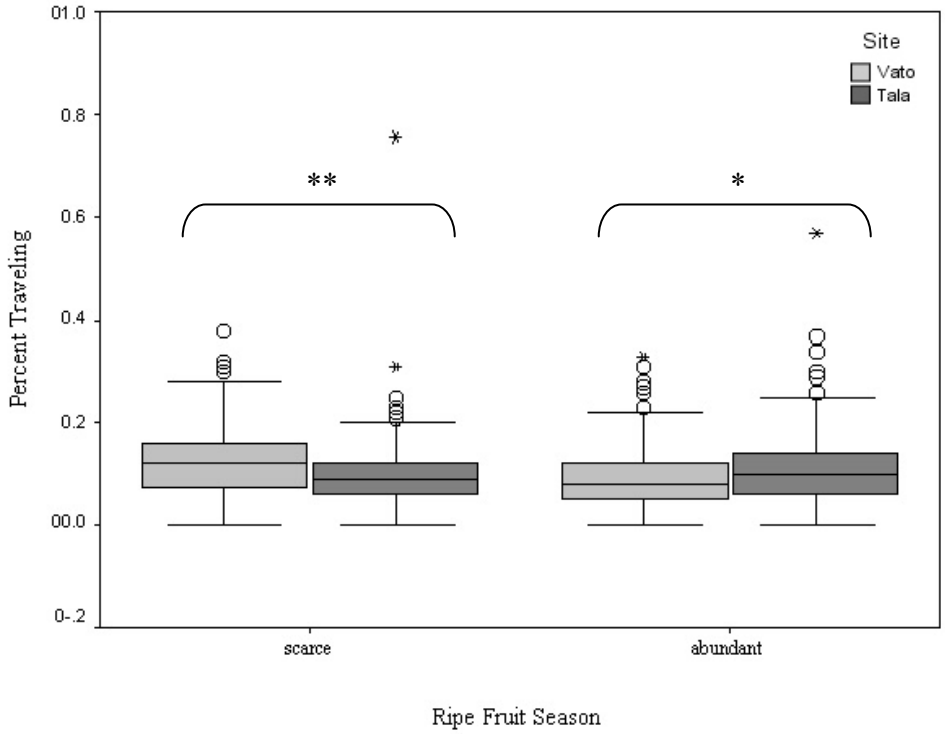


Figure 3.30. Boxplots of relative amount of time spent (A) feeding, (B) resting, and (C) traveling by site. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and circles and stars represent outliers. Sites were significantly different in the scarce season, $F(1,189.49) = 35.698$, $p<.001$, and the abundant season, $F(1,153.810) = 13.554$, $p<.001$.

DISCUSSION

General Time Budget

While frugivorous species typically adopt an energy *maximizing* strategy by spending more time feeding overall (*e.g.,* Dunbar, 1992), these results suggest that *E. rubriventer* adopt a more energy/time minimizing strategy, similar to folivorous species. For instance, folivorous howler monkeys spend 64-80% resting, 10-24% feeding, and 3-12% traveling (Estrada *et al.*, 1999; Rodriguez-Luna *et al.,* 2003). Overall, *Eulemur rubriventer* were energetically conservative and adopted an energy/time minimizing strategy: resting was performed a great deal more than all other behaviors (75.75%), and feeding (11.33%) and traveling (10.53%) were performed a similar amount of time (see also Durham, 2003). Interestingly, the black and white ruffed lemur *(Varecia variegata),* the most frugivorous lemur (Wright, 2006), also spent the majority of time resting (Balko, 1998), and suggest that this may be a strategy of energy conservation. Other behaviors such as social activities were rarely performed by *E. rubriventer* (3.2% grooming**,** 0.18% playing, and 0.002% aggressing). The small proportion of time devoted to social activities, and the even smaller proportion of time devoted to aggression, are typical of the general primate pattern (Sussman *et al.,* 2005)

E. rubriventer's activity budget responded to changes in the environment. Some cathemeral species such as *Eulemur mongoz* alter the proportion of time devoted to nighttime and daytime activity, yet do not vary time budgets seasonally (*e.g.,* Curtis *et al.*, 1999). Despite employing the flexibility of cathemerality like *E. mongoz*, *E. rubriventer* modified the proportion of time spent in each activity with seasonal changes in climate and resources. These divergent results may exist because these species employ

different patterns of cathemerality. While *E. mongoz* are predominantly daytime active during the wet season and nighttime active during the dry season (Curtis *et al.,* 1999), *E. rubriventer* are active during the day and night throughout the year (Overdorff and Rasmussen, 1995). Whereas *E. mongoz* are able to extract similar nutrient content from resources year-round (Curtis, 2004), *E. rubriventer* may employ time budget adjustments to cope with a seasonally changing habitat.

Interestingly, though ripe fruit is the main component of *E. rubriventer*'s diet, their masticatory apparatus resembles that of folivorous species, and their gut passage rate is slower than other frugivorous lemurs (Overdorff and Rasmussen, 1995), indicating that they are able to physically digest and glean nutrients from scarce season diets. Since the digestive needs of *E. rubriventer* are met relatively efficiently and quickly, increased digestion time due to processing unripe fruits and leaves during the lean season may not be required. This may help explain the reduction in time spent resting and increase in time spent feeding during the lean season in this species: more food is required to meet energetic requirements relative to the abundant season, so although more time digesting poorer quality foods may be required, more time resting relative to feeding is not. Therefore, factors such as the amount of activity necessary to forage may impose greater limitations than digestive needs on other activities. Furthermore, *Eulemur mongoz* diets are composed of high fiber content regardless of food item (*e.g.,* ripe fruit, unripe fruit, and leaves). Additional data on the nutrient content of *E. rubriventer* foods will help further our understanding of their energetic strategy.

Patterns of the proportion of time spent in each activity throughout the year emerged. Feeding and resting were consistently inversely related at both sites, as was

also found in howler monkeys *(Alouatta pigra)* (Silver and Marsh, 2003), gelada baboons *(Theropithecus gelada)* (Iwamoto and Dunbar, 1983), and black and white ruffed lemurs *(Varecia variegata variegata)* (Balko, 1998). Although time budgets as they relate to reproductive condition were not analyzed in this study and deserve further attention, feeding peaks and resting troughs occurred during peak weaning and birth periods, and feeding troughs and resting peaks occurred during mid-gestation when food availability was high and declining. These results agree with findings that lemurid appetites wane around mid-April in the southern hemisphere, when temperature and juvenile and hair growth decrease, and remain low until September, the austral spring equinox (Pereira *et al.,* 1999). Thus, energy maximizing strategies were employed during weaning and parturition, the most energetically expensive times for females (Jolly, 1984; Coelho, 1986; Bronson and Heideman, 1994), and a time/energy minimizing strategy was employed during gestation (May – September), a relatively less expensive reproductive stage. One important difference between weaning and birth periods occurred, however: during parturition fruit was scarce, and during weaning fruit was abundant. Feeding for long periods during fruit scarcity is representative of the overall pattern for this species. However, feeding for long periods during fruit abundance may indicate a critical period characterized by either above-average energy requirements, or conversely energy storage. Responses to climate and food availability seasons are discussed below.

Seasonal Time Budget

Climate

Time budgets differed significantly between cool and warm seasons, and between wet and dry seasons. During the cool season *Eulemur rubriventer* adopted an energy

minimizing strategy. In fact, several lemur species rest more during the cool season (Morland, 1993; Schmid and Ganzhorn, 1996; Powzyk, 1997; Wright, 1999). Daytime temperatures may range as much as 15ºC (Richard and Dewar, 1991) and nighttime temperatures can surpass lemurs' thermoneutral zone and require thermoregulatory responses (Curtis *et al.,* 1999). Increased daytime activity and decreased nighttime activity during the cool season have been observed in several cathemeral species (Donati *et al.*, 1999; Rasmussen, 1999; Kappeler and Erkert, 2003; Tarnaud, 2006), and results from this study are consistent with the hypothesis that *less* activity during the coldest time enables the use of body heat to stay warm (*contra* Nash, 1998; Vaanholt *et al.*, 2007). This may be facilitated through huddling (Watts, 1988), which reduces the use of maintenance energy (see Coelho, 1986). Although Overdorff and Rasmussen (1995) found no effect of climate on nighttime movement in *E. rubriventer,* this should not be interpreted to mean that they do not adjust their activity according to temperature fluctuations. Night path length as a measure of activity may obscure differences in the relative proportion of time spent in different behaviors. It is interesting though that while time budgets differed, distance traveled remained the same across seasons (*cf* Overdorff and Rasmussen, 1995). This energy minimizing response was stronger in the Vatoharanana groups who may experience slightly colder temperatures due to the increase in elevation. For instance, Iwamoto and Dunbar (1983) found that as elevation increased, so did gelada baboon *(Theropithecus gelada)* temperature-dependent energy needs.

Likewise, animals may huddle more during the wet season to avoid thermal stress (Watts, 1988). Resting is used as a proxy for huddling since huddling behavior was not

recorded but occurred during the majority of resting bouts (Tecot, personal observation). *E. rubriventer* rested *less* during the wet season.. However, groups in each site responded differently and the Vatoharanana groups rested significantly *more* during this time, as predicted. Alternatively, the wet season may not be a thermally challenging season since it is largely accompanied by warm temperatures.

Time spent feeding and traveling also did not support predictions based upon another frugivorous lemur, *Varecia rubra* (Vasey, 2005). Instead, *E. rubriventer* increased feeding time and decreased traveling time during the wet season. These results may best be explained by fruit availability, which was more variable during the dry season and was accompanied by both high and low feeding times. Previous studies of climate and phenology in primate habitats found that rainfall and fruiting are not related (van Schaik and Pfannes, 2005), and they are not consistently correlated in Ranomafana National Park (Overdorff and Wright, unpublished manuscript; Tecot, Chapter 2). Combined with inverse trends across sites, rainfall season is not on its own a strong influence upon activity budget in this species.

Fruit Availability

No differences between 'total' fruit seasons were found, but time budgets varied across 'ripe fruit' seasons and suggest that ripe fruit exerts a stronger influence upon *E. rubriventer* time budgets (but see below). Overall, *E. rubriventer* are energy/time minimizers in both seasons, spending approximately 75% of their time resting during the lean season, and 79% of their time resting during the abundant season. *E. rubriventer* shifted to a relatively greater energy accumulating strategy during the lean season, traveling and feeding more and resting less. Relative to the abundant season, animals in

both sites maximized food intake rather than further minimizing time and energy expenditure, as predicted by Optimal Foraging Theory (Schoener, 1971). In primates this is the more common response to increased energetic demands (*e.g.,* reproduction; see Hemingway, 1999). Increased time feeding may occur in order to gain sufficient energy from nutrient-poor, less digestible resources, or from a large diversity of rare and patchy foods (Schoener, 1971; Clutton-Brock and Harvey, 1977; Dunbar, 1988; Overdorff, 1988; Passamini, 1998). *E. rubriventer* do shift to a more fibrous, lower quality diet largely consisting of leaves and unripe fruit during the lean season (Overdorff, 1991, 1993a; Tecot, 2007a). Increased time traveling may occur to search for those rare, high quality resources. The decreased availability of nutrients may require greater travel time or distance as animals adjust to the wider, or less predictable, distribution of food (Barton *et al.*, 1992; Garber, 1993; Overdorff, 1993a; Gursky, 2000). This is supported by a study by Overdorff and Rasmussen (1995), where *E. rubriventer* nighttime path lengths varied with time spent feeding during the day. Less time resting may be the sacrifice necessary in order to feed and travel more.

Site Differences

The availability of different food types differs greatly between Vatoharanana and Talatakely (Tecot, Chapter 2). Because of these differences, *Eulemur rubriventer* in Vatoharanana and Talatakely spend different proportions of their time consuming ripe fruit, unripe fruit, and leaves (Tecot, unpublished data). Differences in the nutritional content and distribution of these foods are probable (Altmann *et al.,* 1987; Arrigo-Nelson, 2006) and are likely to impact the amount of time devoted to important social

bonding activities such as grooming (Altmann and Muruthi, 1988; Dunbar, 1992; Balko, 1998; Arrigo-Nelson, 2006).

Contrary to Durham (2003) who found no differences in *Eulemur rubriventer* time budgets between these two sites, this study found significant differences overall and seasonally, which indicate the adoption of different strategies within the bounds of the species-wide energy minimizing strategy. Monthly differences also occurred, and may be attributed to the lack of synchronization in phenological seasonality among sites. It is unknown why these results differ from Durham (2003), but this discrepancy may be attributed to differences in sampling and recording methods (*e.g.,* continuous vs. time interval), or more likely variation in reproduction, climate, and phenology between studies. As inter-annual variation is great in these forests, long-term studies in the future will greatly benefit this type of analysis.

Relative to each other, groups in Vatoharanana, the undisturbed forest, maximized energy intake while Talatakely groups minimized energy expenditure, spending relatively more time resting, less time feeding, and more or less time traveling depending upon the month. Similarly, translocated howler monkeys *(Alouatta pigra)* who were unfamiliar with foods in their new habitat spent more time resting and less time feeding than established groups as they adjusted to their new habitat (Silver and Marsh, 2003). A time budget which maximizes energy relative to another time budget (which necessarily minimizes energy expenditure) may indicate energy storage versus merely filling current energy requirements (Hemingway, 1999). Furthermore, groups in Talatakely spent significantly less time engaged in social behaviors, demonstrating that they are able to devote less of their time to social bonding activities. Social bonding activities are

extremely important in social primates (Sussman *et al.,* 2005), particularly pair-bonded species (Overdorff and Tecot, 2006), because they may reduce several different types of stress (see Sussman *et al.,* 2005). This same trend emerges in *Propithecus edwardsi* groups living in Talatakely, and *Varecia variegata* groups living in Vatoharanana, when compared with groups in Valohoaka, a pristine primary forest site in Ranomafana National Park (Balko, 1998; Arrigo-Nelson, 2006). The finding that Talatakely groups spent less time involved in social activities yet fed for proportionately less time suggests that a strategy of spending less time feeding is not a response to greater availability of high quality foods in that site. If it was, and energy was abundant, more time might be spent performing social behaviors. Social behavior was not analyzed seasonally here because it accounted for very little time, and thus energy. However, more detailed analyses of social behavior will be informative in studies of social stress.

Site differences in seasonal time budgets reflect the flexibility of groups in each site. More significant seasonal variation in activity occurred in Vatoharanana than Talatakely. Similar results have been found for *Lemur catta:* groups in an area characterized by a high incidence of exotic plant species displayed reduced behavioral variation compared with those living in a more natural forest (Rasamimanana and Rafidinarivo, 1993). A greater response to seasonal change in the undisturbed forest may suggest more flexibility (Silver and Marsh, 2003). An alternative explanation for a relatively greater response to seasonal change in Vatoharanana is that there is greater seasonality in that habitat, eliciting a greater behavioral response. Since temperature and rainfall were equivalent, seasonal differences in climate across sites were negligible. Furthermore, phenological changes were considerable in Talatakely (Tecot, Chapter 2),

so the former interpretation is supported by this study. However, it should be noted that Iwamoto and Dunbar (1983) found that as the elevation of gelada baboon *(Theropithecus gelada)* groups increased (and temperature slightly decreased), so did time spent feeding. Although temperature differences between sites in this study were negligible, slight differences in elevation in that study were sufficient to have an effect on feeding time (Iwamoto and Dunbar, 1983). Furthermore, phenological changes in Talatakely were largely *unpredictable* from month to month (Tecot, Chapter 2); fluctuations in food availability in the disturbed forest may occur too rapidly for these groups to adopt alternative strategies as the habitat changes.

Both frugivorous and folivorous primate species living in more degraded habitats frequently spend more time feeding than their primary forest-dwelling counterparts (Milton, 1984; Strier, 1986, 1987; Irwin, 2006). However, differences between Talatakely and Vatoharanana do not support predictions based upon these studies. Inter-site differences in this study were consistent across seasons, and may reflect the relative scarcity of food available overall in Talatakely. For instance, when an environment is degraded and resources are scarce, more time spent resting relative to groups in more pristine habitat may be the only available option to maintain enough energy for survival and reproduction (*cf* Nash, 1998). Therefore, relative to Vatoharanana, the flexibility of energetic strategies employed in Talatakely may be more restricted. More activity throughout the year on the part of animals in Vatoharanana may also help explain higher cortisol levels at this site overall (Tecot, Chapter 4). Alternatively, these differences may be attributed to specific items in the diet. For instance, although *Eulemur rubriventer* are efficient at digesting low quality foods, less digestible foods in Talatakely relative to

Vatoharanana may require relatively more time resting in the disturbed site. Furthermore, significantly more time spent traveling during fruit scarcity by Vatoharanana groups may be explained by the exclusive presence of Chinese guava *(Psidium cattleianum)* in Talatakely, which grows in large stands and may compose up to 100% of the diet during fruit scarcity (Tecot, Chapter 2). Unripe fruit can be composed of difficult to digest fiber and secondary compounds. A diet of 100% unripe guava (Tecot, Chapter 2) may be particularly challenging.

These results assist in identifying pressures affecting how animals spend their time and where they put their energy. This study yielded conflicting results with Irwin's (2006) study of *Propithecus diadema.* He found that groups in fragmented forest adopted an energy maximization strategy, spending more time feeding overall, in contrast with *Eulemur rubriventer* in Talatakely, who spent relatively less time feeding overall when compared with individuals in Vatoharanana. This difference with *Eulemur rubriventer* may be attributed to differences in dietary preference since *Propithecus diadema* is a folivorous species, however *E. rubriventer*'s response to food scarcity was an overall increase in time spent feeding. A similar trend emerged, however, in both studies: during the scarce season group differences were large, but during the abundant season groups in different sites converged on each other (Irwin, 2006), suggesting that as diets overlap (ripe fruit is preferred and abundant) so do time budgets. *Eulemur rubriventer* dietary overlap does in fact decrease greatly during the scarce season (Tecot, 2007a). This result may also suggest that the lean season is a time of strong selective impact, supporting the assertion that low resource periods may be the most critical times for primates (Milton,

1982; Terborgh, 1983, 1986ab; Chapman and Chapman, 1999; Brugiere *et al.,* 2002), particularly frugivores.

CONCLUSIONS

Although *Eulemur rubriventer* feed upon ripe fruit approximately 75% of the time (Tecot, this study), they adopt an energy minimizing time budget typical of folivores. This does not appear to be due to digestive restrictions, and may indicate restricted energy sources in the environment. This species' behavior is particularly plastic, however. This study found that, in addition to modifying their behavior throughout the 24-hour cycle (Overdorff and Rasmussen, 1995), *E. rubriventer* vary the proportion of time spent performing different behaviors in response to rainfall, temperature, and food availability. Moreover, populations in different sites subject to variable seasonality of food resources may respond differently to similar climate changes. The relationship between gross energy (food) and maintenance energy (thermoregulation) depends upon and influences metabolic rates and behavioral budgets. This species is able to fine-tune its energetic expenditure and intake to accommodate the very particular environmental circumstances it encounters at any given time.

Within an overall energy minimizing strategy, relative to populations in disturbed forest, *Eulemur rubriventer* in undisturbed forest adopted a time budget geared towards maximizing energy, indicating that a more predictable food base enables this species to store energy when it is abundant. Likewise, resource-challenged populations may be relatively less active as they are only able to fill current energetic requirements. Particularly in unpredictable environments, the ability to store energy may greatly impact reproductive success. In fact, during the most energetically expensive times of the year (late lactation, weaning), both populations of this species utilized a relatively greater

energy maximizing strategy. These results indicate that a greater ability to *maximize resources* during critical times, as was seen in undisturbed populations, provides a great benefit. It is clear that this species' ability to accommodate changing needs is well developed. Furthermore, phenological and climatological fluctuations at these two sites have been established (Tecot, Chapter 1). Thus, a relatively small divergence from the species mean time budget, as demonstrated by weaker behavioral modifications across seasons in the disturbed population, indicates the presence of an environmental-level, rather than a species-level, constraint.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*. 49:227-267.

Altmann, J. and Muruthi, P. 1988. Differences in daily life between semi-provisioned and wild feeding baboons. *American Journal of Primatology*. 15:213-221.

Altmann, S.A., Post, D.G., Klein, D.F. 1987. Nutrients and toxins of plants in Amboseli, Kenya. *African Journal of Ecology*. 25:279-293.

Arrigo-Nelson, S.J. 2006. *The Impact of Habitat Disturbance on the Feeding Ecology of the Milne-Edwards' Sifaka (*Propithecus edwardsi*) in Ranomafana National Park* [Doctoral Dissertation]. Stony Brook, NY: Stony Brook University, 181 p.

Aschoff, J. Survival value of diurnal rhythms. In: O.G. Edholm, editor; 1964; London. Symposium of the Zoological Society of London. Pp. 79–98.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Balko, E.A. 1998. *A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by* Varecia variegata variegata *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Syracuse, NY: SUNY-CESF. 245 p.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W., Simpson, A.J. 1992. Habitat use and resource availability in baboons. *Animal Behaviour*. 43:831-844.

Bearder, S.K., Nekaris, K.A.I., Curtis, D.J. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatologica*. 77:50-71.

Bicca-Marques, J.C., Calegaro-Marques, C. 1998. Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology*. 106(4):533-546.

Bicca-Marques, J.C. and Calegaro-Marques, C. 1994. Activity budget and diet of *Alouatta caraya*: An age-sex analysis. *Folia Primatologica*. 63(4):216-220.

Boinski, S. 1987. Habitat use by squirrel monkeys in a tropical lowland forest. *Folia Primatologica*. 49:151-167.

Boinski, S., Ehmke, E., Kauffman, L., Schet, S., Vreedzaam, A. 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis and S. sciureus*): II. Within-species and local variation. *Behaviour*. 142:633-677.

Brugiere, D., Gautier, J.P., Moungazi, A., Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *International Journal of Primatology*. 23(5):999-1024.

Carrillo, E., Saenz, J.C., Fuller, T.K. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. *Biological Conservation*. 108(3):317-324.

Chapman, C.A. and Chapman, L.J. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*. 40:215-231.

Clutton-Brock, T.H., Harvey, P.H. 1977. *Primate Ecology*. T.H. Clutton-Brock, editor. London: Academic Press.

Clutton-Brock, T.H., Harvey, P.H., Rudder, B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*. 269:797-800.

Coelho, A.M. 1986. Time and energy budgets. In: G. Mitchell, J. Erwin, editors. *Comparative primate biology*. New York: Alan R. Liss. p 141–166.

Colquhoun, I.C. 1998. Cathemeral behavior of *Eulemur macaco macaco* at Ambato Massif, Madagascar. *Folia Primatologica*. 69(S1):22-34.

Colquhoun, I.C. 2006. Predation and cathemerality: Comparing the impact of predators on the activity patterns of Lemurids and Ceboids. *Folia Primatologica*. 77:143-165.

Curtis, D.J. 2004. Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology*. 124(3):234-247.

Curtis, D., Zaramody, A, Martin, RD. 1999. Cathemerality in the Mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology*. 47:279–298.

Curtis, D.J. and Rasmussen, M.A. 2002. Cathemerality in lemurs. *Evolutionary Anthropology*. S1:83-86.

Curtis, D.J. and Rasmussen, M.A. 2006. The evolution of cathemerality in primates and other mammals: A comparative and chronoecological approach. *Folia Primatologica*. 77(1-2):178-193.

Cuthill, I. and Houston, A.I. 1997. Managing time and energy. In: JR Krebs, Davies, NB, editors. *Behavioural Ecology: An Evolutionary Approach*. Massachusetts: Blackwell Science. Pp. 97-120.

DaGosto, M. 1989. Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 78:209.

Dasilva, G.L. 1992. The western black-and-white colobus as a low-energy strategist: Activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology*. 61(1):79-91.

Dausmann, K., Glos, J., Ganzhorn, J.U., Heldmaier, G. 2004. Hibernation in a tropical primate. *Nature*. 429:825-826.

Defler, T.R. 1995. The time budget of a group of wild woolly monkeys *(Lagothrix lagotricha)*. *International Journal of Primatology*. 16(1):107-120.

Dewar, R. and Wallis, J.R. 1999. Geographical patterning of interannual rainfall variability in the tropics and near tropics: An L-moments approach. *Journal of Climate*. 12(12):3457-3466.

DiFiore, A. and Rodman, P.S. 2001. Time allocation patterns of lowland woolly monkeys *(Lagothrix lagotricha poeppigii)* in a neotropical terra firma forest. *International Journal of Primatology*. 22:449–480.

Donati, G. and Borgognini-Tarli, S. M. 2006. Influence of abiotic factors on cathemeral activity: The case of *Eulemur fulvus collaris* in the littoral forest of Madagascar. *Folia Primatologica*. 77(1-2):104-122.

Donati, G., Lunardini, A., Kappeler, P.M. 1999. Cathemeral activity of red-fronted brown lemurs *(Eulemur fulvus rufus)* in the Kirindy Forest/CFPF. *New Directions in Lemur Studies*. New York: Kluwer Academic/Plenum Press. Pp. 119-137.

Doran, D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology*. 18(2):183-206.

Dunbar, R.I.M. 1988. *Primate Social Systems*. Ithaca, New York: Cornell University Press, 373 p.

Dunbar, R.I.M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*. 31(1):35-49.

DuPuy, D.J. and Moat, J. 1995. A refined classification of the primary vegetation based on the underlying geology: Using GIS to map its distribution and to assess its

conservation status. In: W.R. Laurenco, editor. *Biogeography of Madagascar*. Paris: Unesco. Pp. 205-218.

Durham, D.L. 2003. *Variation in responses to forest disturbance and the risk of local extinction: A comparative study of wild* Eulemurs *at Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Davis: University of California, Davis, 170 p.

Ebensperger, L.A. and Hurtado, M.J. 2005. Seasonal changes in the time budget of degus, *Octodon degus*. *Behaviour*. 142:91-112.

Engqvist, A. and Richard, A.F. 1991. Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatologica*. 57:169-172.

Erkert, H.G. and Cramer, B. 2006. Chronobiological background to cathemerality: Circadian rhythms in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). *Folia Primatologica*. 77(1-2):87-103.

Estrada, A., Juan-Solano, S., Ortíz Martínez, T., Coates-Estrada, R. 1999. Feeding and general activity patterns of a howler monkey *(Alouatta palliata)* troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology*. 48(3):167-183.

Fairgrieve, C. and Muhumuza, G. 2003. Feeding ecology and dietary differences between blue monkey *(Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *African Journal of Ecology*. 41:141-149.

Fernandez-Duque, E. and Erkert, H.G. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinean Chaco. *Folia Primatologica*. 77:123–138.

Fox, E.A., Van Schaik, C.P., Sitompul, A., Wright, D.N. 2004. Intra- and interpopulational differences in orangutan *(Pongo pygmaeus)* activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*. 125(2):162-174.

Ganzhorn, J., Wright, P.C., Ratsimbazafy, H.J. 1999b. Primate communities: Madagascar. In: JG Fleagle, Janson, CH, Reed, K, editor. *Primate Communities*. Cambridge: Cambridge University Press. Pp. 75-89.

Ganzhorn, J.U. 1995a. Cyclones over Madagascar: Fate or fortune? *Ambio*. 24:124-125.

Ganzhorn, J.U., Fietz, J., Rakotovao, E., Schwab, D., Zinner, D. 1999a. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*. 13:794-804.

Garber, P.A. 1993. Seasonal patterns of diet and range in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology*. 14:145-166.

Geiser, F. and Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology*. 68:935–966.

Gelatt, T.S., Siniff, D.B., Estes, J.A. 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *Journal of Wildlife Management*. 66(1):29-39.

Glander, K.E. 1981. Feeding patterns in mantled howling monkeys In: A. Kamil and T. Sargent, editors. *Foraging Behavior: Ecological and Psychological Approaches*. New York: Garland Press. Pp. 231-258.

Glander, K.E., Wright, P.C., Daniel, P.S., Merenlender, A.M. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *Journal of Human Evolution*. 22:1-17.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*. 123:250-276.

Gould, L., Sussman, R.W., Sauther, M.L. 1999. Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs *(Lemur catta)* in southwestern Madagascar. *International Journal of Primatology*. 20(1):69-84.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Green, G.M. and Sussman, R.W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*. 248:212-215.

Gursky, S. 2000. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*. 21:477-495.

Halle, S. and Stenseth, N.C. 2000. *Activity Patterns of Small Mammals: An Ecological Approach*. Berlin: Springer, 322 p.

Halle, S. 2006. Polyphasic Activity Patterns in Small Mammals. *Folia Primatologica*. 77(1-2):15-26.

Hammond, K.A. and Diamond, J. 1997. Maximal sustained energy budgets in humans and animals. *Nature*. 386:457-462.

Hanya, G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: Effects of food and temperature. *American Journal of Primatology*. 63:165-177.

Harcourt, A. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: T. Caro, editor. *Behavioral Ecology and Conservation Biology*. New York: Oxford University Press. Pp. 56-79.

Harcourt, C. and Thornback, J. 1990. *Lemurs of Madagascar and the Comoros. The IUCN Red Data Book*. Gland, Switzerland: IUCN. 240 p.

Harcourt, C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *Journal of Zoology*. 223:667-674.

Hemingway, C.A. 1995. *Feeding and Reproductive Strategies of* Propithecus diadema edwardsi [Doctoral Dissertation]. Durham: Duke University.

Hemingway, C.A. 1999. Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? *Behavioral Ecology and Sociobiology*. 45:311-322.

Hemingway, C.A. and Bynum, N. 2005. The influence of seasonality on primate diet and ranging. In: D.K. Brockman, van Schaik, C.P., editor. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 57-104.

Hemingway, C.A. and Overdorff, D.J. 1999b. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. *Biotropica*. 31:354-364.

Hennessy, M.B., Mendoza, S.P., Mason, W.A., Moberg, G.P. 1995. Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*. 57(2):331-338.

Hill, R.A. 2005. Day length seasonality and the thermal environment. D.K. Brockman and C.P. van Schaik, editors. *In Primate Seasonality: Implications for Human Evolution*. Cambridge: Cambridge University Press. Pp. 197-213.

Hill, R.A. 2006. Why be diurnal? Or, why not be cathemeral? *Folia Primatologica*. 77:72-86.

Hwang, M.H. and Garshelis, D.L. 2007. Activity patterns of Asiatic black bears *(Ursus thibetanus)* in the Central Mountains of Taiwan. *Journal of Zoology*. 271(2):203-209.

Irwin, M.T. 2006. *Ecological Impacts of Forest Fragmentation on Diademed Sifakas* (Propithecus diadema) *at Tsinjoarivo, eastern Madagascar: Implications for Conservation in Fragmented Landscapes* [Doctoral Dissertation]. Stony Brook, New York: Stony Brook University, 410 p.

Irwin, M.T. 2007. Living in forest fragments reduces group cohesion in Diademed Sifakas *(Propithecus diadema)* in Eastern Madagascar by reducing food patch size. *American Journal of Primatology*. 69:434-447.

Irwin, M.T., Johnson, S.E., Wright, P.C. 2005. The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx*. 39(2):204-218.

IUCN. 2006. *2006 IUCN Red List of Threatened Species*.

Iwamoto, T. and Dunbar, R.I.M. 1983. Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *The Journal of Animal Ecology*. 52(2):357-366.

Johns, A.D. and Skorupa, J.P. 1987. Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*. 8(2):157-191.

Johnson, S.E. and Overdorff, D.J. 1999. Census of brown lemurs (*Eulemur fulvus spp*.) in southeastern Madagascar: Methods-testing and conservation implications. *American Journal of Primatology*. 47(1):51-60.

Kappeler, P.M. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*. 57(3):132-146.

Kappeler, P.M., Erkert, H.G. 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs *(Eulemur fulvus rufus)*. *Behavioural Ecology and Sociobiology*. 54:359–369.

Kenagy, G.J., Sharbaugh, S.M., Nagy, K.A. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia*. 78(2):269-282.

Keuroghlian, A. 2003. *The Response of Peccaries to Seasonal Fluctuations in an Isolated Patch of Tropical Forest* [Doctoral Dissertation]. Reno, Nevada: University of Nevada, 158 p.

Kleiber, M. 1961. *The Fire of Life: An Introduction to Animal Energetics*. New York: Wiley.

Kuntz, R., Kubalek, C., Ruf, T., Tataruch, F., Arnold, W. 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse *(Equus ferus przewalskii)*. *The Journal of Experimental Biology*. 209:4557-4565.

Le Maho, Y., Goffart, M., Rochas, A., Felabel, H., Chatonnet, J. 1981. Thermoregulation in the only nocturnal simian: the night monkey *Aotus trivirgatus*. *American Journal of Physiology*. 240:R156-R165.

Marsh, C.W., Johns, A.D., Ayres, J.M. 1987. Effects of habitat disturbance on rain forest primates. In: C.W. Marsh and R.A. Mittermeier, editors. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 83-107.

Merenlender, A.M. 1993. *The Effects of Sociality on the Demography and Genetic Structure of* Lemur fulvus rufus *(Polygamous) and* Lemur *(Monogamous) and the Conservation Implications* [Doctoral Dissertation]. Rochester, New York: University of Rochester.

Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes.* Washington, DC: Smithsonian Institution Press. Pp. 273-289.

Milton, K. 1984. Habitat, diet, and activity patterns of free-ranging woolly spider monkeys *(Brachyteles arachnoides:* E. Geoffroy 1806). *International Journal of Primatology*. 5(5):491-514.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersalll, I., Meyers, D.M. 2006. *Lemurs of Madagascar, 2nd Edition*. Washington, DC: Conservation International, 520 Pp.

Morland, H.S. 1991. Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rainforest. *Folia Primatologica*. 56:157-161.

Morland, H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 193-203.

Morton, E.S. 1977. Intratropical migration in the Yellow-green Vireo and Piratic Flycatcher. *The Auk*. 94:97-106.

Mourão, G. and Medri, Í.M. 2007. Activity of a specialized insectivorous mammal *(Myrmecophaga tridactyla)* in the Pantanal of Brazil. *Journal of Zoology*. 271:187-192.

Nash, L.T. 1998. Vertical clingers and sleepers 1 : Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*. 69(Suppl. 1):204-217.

Neville, M.K., Glander, K.E., Braza, F., Rylands, A.B. 1988. The howling monkeys, Genus *Alouatta*. In: R.A. Mittermeier, A.B. Rylands, A.F. Coimbra-Filho, G.A.B.

de Fonesco, editors. *Ecology and Behavior of Neotropical Primates*: World Wildlife Fund. Pp. 349-454.

Nielsen, E.T. 1983. Relation of behavioural activity rhythms to the changes of day and night. A revision of views. *Behavioural Processes*. 89:147–173.

Norscia I., Carrai V., Borgognini-Tarli S.M. 2006. Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*. 27:1001-1022.

Oates, J.F. 1977. The guereza and its food. In: T.H. Clutton-Brock, editor. *Primate Ecology*. London: Academic Press. Pp. 276-319.

Onderdonk, D.A. and Chapman, C.A. 2000. Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology*. 21:587-611.

Overdorff, D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D.J. 1991. *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral Dissertation]. Durham: Duke University, 313 p.

Overdorff, D.J. 1993a. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. *International Journal of Primatology*. 14(5):721-753.

Overdorff, D.J. 1993b. Ecological and reproductive correlates with ranging patterns in two prosimian primates in Madagascar. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 167-192.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40:327-342.

Overdorff, D.J. 1996b. Ecological correlates to social structure in two lemur species in Madagascar. *American Journal of Physical Anthropology*. 100(4):487-506.

Overdorff, D.J. and Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Overdorff, D.J. and Tecot, S. R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M.L. Sauther, editors. *Lemurs: Ecology and Adaptation*. New York: Springer. p 235-245.

Overdorff, D.J. and Johnson, S. 2003. *Eulemur*, true lemurs. . In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1320-1324.

Overdorff, D.J. and Rasmussen, M.A. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 61-74.

Passamini, M. 1998. Activity budget of Geoffroy's Marmoset *(Callithrix geoffroyi)* in an Atlantic forest in Southeastern Brazil. *American Journal of Primatology*. 46:333-340.

Pereira, M. 1993. Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 205-221.

Pereira, M.E., Strohecker, R.A., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. *New Directions in Lemur Studies*. New York: Kluwer Academic/Plenum. Pp. 93-118.

Peres, C.A. 1994. Primate responses to phenological changes in an Amazonian terre firme forest. *Biotropica*. 26(1):98-112.

Petter-Rousseaux, A. 1980. Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In: P. Charles-Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, J.-J. Petter, A. Schilling, editors. *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*. New York: Academic Press. Pp. 137-152.

Pochron, S.T. 2000. Sun avoidance in the yellow baboons *(Papio cynocephalus cynocephalus)* of Ruaha National Park, Tanzania. Variations with season, behaviour and weather. *International Journal of Biometeorology*. 44:141–147.

Pollack, J.I. 1979. Spatial distribution and ranging behavior in lemurs. In: G.A. Doyle, R.D. Martin, editors. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 359–409.

Poulsen, J.R., Clark, C.J., Smith, T.B. 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*. 54:91-105.

Powzyk, J.A. 1997. *The Socio-ecology of Two Sympatric Indriids:* Propithecus diadema diadema *and* Indri indri, *a Comparison of Feeding Strategies and Their Possible Repercussions on Species-Specific Behaviors* [Doctoral Dissertation]. Durham, NC: Duke University.

Rasamimanana, H.R. and Rafidinarivo, E. 1993. Feeding behavior of Lemur catta females in relation to their physiological state. Lemur Social Systems and Their Ecological Basis. New York: Plenum Press. Pp. 123-133.

Rasmussen, M.A. 1999. *Ecological Influences on Activity Cycle in Two Cathemeral Primates,* Eulemur mongoz *(Mongoose Lemur) and* Eulemur fulvus fulvus *(Common Brown Lemur)* [Doctoral Dissertation]. Durham, N.C.: Duke University.

Richard, A.F. 1978. Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi:* Lemuriformes. In: G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Washington, D.C.: Smithsonian Institute Press. Pp. 519-533.

Richard, A.F. and Sussman, R. W. 1987. Framework for primate conservation in Madagascar. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 329-341.

Richard, A.F. and Dewar, R.E. 1991. Lemur ecology. *Annual Review of Ecology and Systematics.* 22:145–175.

Richard, A.F. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Richter, H.V. and Cumming, G.S. 2006. Food availability and annual migration of the straw-colored fruit bat *(Eidolon helvum)*. *Journal of Zoology*. 268(1):35-44.

Ricklefs, R.E. and Miller, G. L. 2000. *Ecology*. New York: W. H. Freeman and Company, 822 p.

Riley, E.P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*. 28(1):107-133.

Rodríguez-Luna, E., Domínguez-Domínguez, L.E., Morales-Mávil, J.E., Martínez-Morales, M. 2003. Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island. In: L.K. Marsh, editor. *Primates in Fragments: Ecology and Conservation*. New York: Kluwer Academic/Plenum Publishers. Pp. 229-250.

Sauther, M.L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ringtailed lemur conservation. *Folia Primatologica*. 69:309-320.

Schmid, J. 1998. Daily torpor in mouse lemurs, *Microcebus* spp.: Metabolic rate and body temperature. *Folia Primatologica*. 69:394-404.

Schmid, J. and Kappeler, P.M. 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur *(Microcebus murinus)*. *Behavioural Ecology and Sociobiology*. 43:125-132.

Schmid, J., Stephenson, P.J. 2003. Physiological adaptations of Malagasy mammals: Lemurs and tenrecs compared. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1198-1203.

Schmid, J. and Ganzhorn, J.U. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. *American Journal of Primatology*. 38:169-174.

Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*. 2:369-404.

Silver, S.C. and Marsh, L.K. 2003. Dietary flexibility, behavioral plasticity, and survival in fragments: lessons from translocated howlers. In: L.K. Marsh, editor. *Primates in Fragments: Ecology in Conservation*. New York: Kluwer Academic/Plenum. Pp. 251-265.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. San Francisco: W.H. Freeman, 859 p.

Sørg, J.-P., Ganzhorn, J.U., Kappeler, P.M. 2003. Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestiere. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1512-1519.

Stephenson, P.J. 2003. Lipotyphla (ex Insectivora): *Geogale aurita,* large-eared tenrec. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. p 1265-1273.

Stoner, K.E. 1996. Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys *(Alouatta palliata)* in northeastern Costa Rica. *International Journal of Primatology*. 17(1):1-30.

Strier, K.B. 1986. *The Behavior and Ecology of the Woolly Spider Monkey, or Muriqui* (Brachyteles arachnoides) [Doctoral Dissertation]. Cambridge, MA: Harvard University.

Strier, K.B. 1987. Activity budgets of Woolly Spider monkeys or Muriquis *(Brachyteles arachnoides)*. *American Journal of Physical Anthropology*. 13:385-195.

Struhsaker, T.T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation*. Gainesville: University Press of Florida.

Sussman, R.W. 1974. Ecological distinctions in sympatric species of *Lemur*. In: R.D. Martin, G.A. Doyle, A.C. Walker, editors. *Prosimian Biology*. London: Duckworth.

Sussman, R.W., Garber, P.A., Cheverud, J.M. 2005. Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology*. 128(1):84-97.

Tarnaud, L. 2006. Cathemerality in the Mayotte Brown Lemur *(Eulemur fulvus)*: Seasonality and food quality. *Folia Primatologica*. 77(1-2):166-177.

Tattersalll, I. 1976. Group structure and activity rhythm in *Lemur mongoz* (Primates, Lemuriformes) on Anjouan and Moheli islands, Comoro archipelago. *Anthropological Papers of the American Museum of Natural History*. 53:363–378.

Tattersalll, I. 1987. Cathemeral activity in primates - a definition. *Folia Primatologica*. 49(3-4):200-202.

Tattersalll, I. 2006. The concept of cathemerality: History and definition. *Folia Primatologica*. 77(1-2):7-14.

Taylor, C.R., Heglund, N.C., Maloiy, G.M. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*. 97:1-21.

Tecot, S. 2006. Activity budget and microhabitat in *Eulemur rubriventer*. *American Journal of Primatology*. 68(1):111-112.

Tecot, S. 2007. Seasonality, phenology, and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. S44:230.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Tecot, S. and Overdorff, D. 2006. The influence of feeding behavior on reproduction in *Eulemur rubriventer* in SE Madagascar. *American Journal of Physical Anthropology*. S42:175.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton, N.J.: Princeton University Press.

Terborgh, J. 1986a. Community aspects of frugivory in tropical forests. In: A. Estrada and T.H. Fleming, editors. *Frugivores and Seed Dispersal*. Dordrecht: Dr. W. Junk Publishers. Pp. 372-384.

Terborgh, J. 1986b. Keystone plant resources in the tropical forest. In: M.E. Soulé, editor. *Conservation Biology, the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc.. Pp. 330–344.

Terranova, C.J. and Coffman, B.S. 1997. Body weights of wild and captive lemurs. *Zoo Biology*. 16(1):17-30.

Tsuji, Y., Fujita, S., Sugiura, H., Saito, C., Takatsuki, S. 2006. Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. *American Journal of Primatology*. 68:1068-1080.

Turk, D. 1995. *A Guide to the Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Vaanholt, L.M., Garland, T., Jr., Daan, S., Visser, G.H. 2007. Wheel-running activity and energy metabolism in relation to ambient temperature in mice selected for high wheel-running activity. *Journal of Comparative Physiology*. 177:109-118.

van Schaik, C.P. and Pfannes, K.R. 2005. Tropical climates and phenology: a primate perspective. In: D.K. Brockman, C. P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 23-54.

van Schaik, C.P. and Kappeler, P.M. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*. 102:915-941.

Vasey, N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons:* I. Interspecific patterns. *American Journal of Physical Anthropology*. 112(3):411-431.

Vasey, N. 2004. Circadian rhythms in diet and habitat use in red ruffed lemurs *(Varecia rubra)* and white-fronted brown lemurs *(Eulemur fulvus albifrons)*. *American Journal of Physical Anthropology*. 124(4):353-363.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs *(Varecia rubra)* on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. *American Journal of Primatology*. 66(4):393-394.

Watts, D.P. 1988. Environmental influences on Mountain gorilla time budgets. *American Journal of Primatology*. 15:195-211.

White, F., Overdorff, D.J., Balko, E., Wright, P.C. 1995. Distribution of ruffed lemurs *(Varecia variegata)* in Ranomafana National Park, Madagascar. *Folia Primatologica*. 64:124-131.

Wright, P.C. 1992. Primate ecology, rainforest conservation, and economic development: Building a national park in Madagascar. *Evolutionary Anthropology*. 1(1):25-33.

Wright, P.C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 16(5):835-854.

Wright, P.C. and Martin, L.B. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: L. Alterman, G.A. Doyle, M.K. Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum. Pp. 45-60.

Wright, P.C. 1997. The future of biodiversity in Madagascar: A view from Ranomafana National Park. In: S. G. Goodman and B. D. Patterson, editors. *Natural Change and Human Impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press. Pp. 381-405.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*. 42:31-72.

Wright, P. 2006. Considering climate change effects in lemur ecology and conservation. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 385-401.

Young, A.L., Richard, A.F., Aiello, L.C. 1990. Female dominance and maternal investment in Strepsirrhine primates. *American Naturalist*. 135:473-488.

Chapter 4: Fecal Cortisol Levels in *Eulemur rubriventer*: Physiologically Coping with Environmental Heterogeneity

INTRODUCTION

Physiological Stress

The vertebrate endocrine system and its response to stress have been studied for several decades. Selye (1950) first postulated that the stress response helps the body achieve homeostasis and is nonspecific: glucocorticoids are secreted in response to many different types of stressors. In other words, a physiological, environmental, or psychosocial stressor will all produce the same response within the vertebrate endocrine system. Subsequent research suggests that the stress response is more specific than Selye (1950) first suggested and depends upon how stress is perceived by the organism. For instance, the body experiences and overcomes gradual stress such as seasonal temperature changes by slight physiological changes which *maintain* homeostasis. However, sudden or unpredictable stressors such as a predation event initiate a response which helps *reestablish* homeostasis (Sapolsky, 1994; Chrousos *et al.*, 1998; Nelson and Klein, 1999; see Selye, 1980; for views on the utility of the stress concept and the replacement of 'stress response' with 'allostatic response', see Sterling and Eyer, 1988; Dallman, 2003, McEwen and Wingfield, 2003ab, Schulkin, 2003, Walsberg, 2003). This type of response may be initiated by both natural disturbances (such as environmental change, predation, and social instability), and anthropogenic disturbances (such as noise and habitat alteration).

Essentially all vertebrates have evolved physiological coping adaptations which allow them to respond to energetically demanding (stressful) conditions. The perception of a stressor by an individual initiates a suite of behavioral and physiological responses including the release of glucocorticoids in the hypothalamic-pituitary-adrenal (HPA) axis (Figure 4.1). The stress response is an extensive and intricate process involving the immune, endocrine, and central nervous systems, and has been reviewed in detail by Chrousos (1998). One aspect of the stress response involves the organs of the HPA axis, which are stimulated to secrete chemical messengers (*e.g.,* hormones and neurotransmitters) which stimulate and regulate other chemical messengers and are capable of suppressing certain physiological functions deemed unnecessary during the stress response. A negative feedback loop down-regulates itself as the stressor subsides and the body copes (*e.g.,* behaviorally). During this process glucocorticoids such as cortisol are secreted by the adrenal cortex into the blood to help ensure that adequate energy is available (*i.e.,* fats and amino acids are mobilized) to meet increased metabolic demands, in proportion to the stressor's intensity (Hennessy *et al.,* 1979), and these serve to initiate behavioral responses. Glucocorticoids are likely to help improve overall reproductive success, and have even been termed 'anti-stress hormones' (Wingfield and Kitaysky, 2002) because they help individuals cope with stress.

Stress and Darwinian Fitness

Both acute and chronic stressors affect the HPA axis and the interaction between hormones and behavior. Determining how proximate mechanisms are at work is critical to understanding how species reconcile the competing needs of reproduction and survival in a dynamic environment. Due to the effects of stress on longevity and reproduction, the

study of stress also has wide-ranging implications for reproductive success. Hormonal assessments can help identify reproductive constraints, and the selective pressures that have influenced the evolution of different reproductive strategies (Whitten *et al.*, 1998a).

Although the term 'stress' carries negative connotations, the stress response evolved because it is adaptive. For instance, acute stress responses help organisms mobilize energy in emergency situations. Energy is temporarily redirected away from long-term survival functions (Sapolsky, 1987) which are deemed unnecessary during the stress response, such as reproduction (Coe *et al.,* 1982; Sapolsky, 1985; Wingfield *et al.,* 1997), territorial behavior (Wingfield *et al.,* 1997), and immune function (Cohen, 1988; Khansari *et al.,* 1990; Dobbin *et al.,* 1991), and toward the immediate needs of the organism (Chrousos, 1998). When exposed to an acute stressor, the cost of temporary inhibition of these long-term functions is generally outweighed by the benefit of energy mobilization, and ultimately this response may increase reproductive success by helping individuals through emergencies such as a predation event (Lee and Cockburn, 1985), and by helping individuals avoid chronic stress through the initiation of behavioral responses (Breuner *et al.*, 1999). Identifying periods in which the stress response is launched can help identify periods when species are internally responding to external pressures.

However, the actions of glucocorticoids may become maladaptive when individuals are subject to chronic (weeks to months) stressors (Selye, 1956; Coe and Scheffler, 1989; Sapolsky, 1994). When mammals undergo a negative energy balance, reproductive function is impaired (Bronson, 1999). *Prolonged* stress suppresses reproduction to the point that it may cause impotence, anovulation, and loss of libido

(Sapolsky, 1992). While rises in the glucocorticoid cortisol during reproductive periods may co-occur with increased fertility (Bercovitch and Ziegler, 2002; Moore and Jessop, 2003), cortisol secretion associated with reproduction may increase to higher levels in response to induced stress (Saltzman *et al.,* 1994), and cortisol has been found to inhibit female primates' ability to reproduce (Wasser and Starling, 1988; Mendoza and Mason, 1988; Chatterton *et al.,* 1991; Sapolsky, 1992; Cameron, 1997; Bronson, 1999). Prolonged stress may also inhibit immune function and affect susceptibility to parasite infestation and disease (Cohen, 1988; Esch *et al.,* 1975; Keller *et al.,* 1983; Laudenslager *et al.,* 1983, Chapman *et al.*, 2006; Muehlenbein, 2006), which can in turn increase energy expenditure, decrease digestion, and reduce reproductive output (Coop and Holmes, 1996). Extended activation of the HPA axis is likely to result in detrimental fitness consequences in a wide range of vertebrate species [*e.g., reproductive failure*: Arnold and Dittami, 1997 (marmots), Sapolsky, 1985 (primates); *abandonment of offspring, reduced survival of young, increased mortality*: Colwell *et al.,* 1988, Rodway *et al.,* 1996, Cotter and Gratto, 1995 (birds), Pride, 2005b (primates); *decline in longevity*: Burrows *et al.,* 1994 (wild dogs)]. Hormonal analyses are a promising avenue of research to better assess the relationships between the environment, stress, and reproductive success, as they can identify periods of challenge, the strategies with which species cope, and the parameters exerting strongest selective pressure.

It should be noted that although the term ‘stress’ is the subject of wide debate due to its negative connotation, the term will be used here to refer to any time a stress response is launched. Although the stress response can become maladaptive if prolonged, periods of stress do not necessarily indicate periods of energetic suffering

such that not enough nutrients are available for maintenance and production. Rather, periods of stress, if not pathological, indicate nutrient partitioning and successful adaptation to the challenges of the environment such that animals can survive and reproduce. Measuring the stress response can identify environmental challenges and the mechanisms which shape life history strategies as we see them today.

Measuring Stress: Cortisol

While a number of indicators have been used to assess stress levels, glucocorticoids such as cortisol and corticosterone are currently considered one of the most reliable and widely applied measures. A variety of other measures have been used but found limited in their abilities to detect stress. For instance, though heart rate is a dependable indicator of metabolic rate, it may not always reflect a stress response (Harlow *et al.,* 1987; Hofer and East, 1998), and is not able to measure the effects of long-term stress. Several studies of vertebrate taxa determined that behavioral data were less sensitive than cortisol measures in recording psychosocial stress events (Coe *et al.,* 1982; Paterson and Pearce, 1992; Schapiro *et al.,* 1993; Clarke *et al.,* 1996; Gust *et al.,* 1996; Smith and French, 1997; Walker *et al.,* 2005; but see Mendoza and Mason, 1988). Population density has also been used as a measure of stress (Glessner and Britt, 2005). Crowding-induced stress may result in low population densities indicating a stressful environment incapable of supporting a higher density. However, population density alone is not an ideal indicator of stress because population numbers often remain high when habitats shrink or decline in quality (Hofer and East, 1998). Catecholamines (adrenaline, dopamine) may be the most ideal measure of stress. During a stress response they are released prior to cortisol and represent a more immediate response. However,

this very attribute (represented by a rapid and transient rise) makes it difficult to accurately measure catecholamine levels and capture the stress response (Hofer and East, 1998). Consequently, glucocorticoid levels are one of the most frequently employed indicators of stress (for reviews see Whitten *et al.* 1998a; Möstl and Palme, 2002; Millspaugh and Washburn, 2004; Strier and Ziegler, 2005; Ziegler and Wittwer, 2005; Honess and Marin, 2006; Keay *et al.*, 2006). Cortisol levels increase in direct proportion to the intensity of the stressor (Hennessey *et al.*, 1975), and long-term measures of glucocorticoids can identify patterns of stress sensitivity in response to environmental changes, which can ultimately identify selection pressures that have shaped species, and that may in turn affect their future fitness.

Daily and Seasonal Cortisol Profiles in Vertebrates

Glucocorticoids may fluctuate both daily and seasonally (*black bears*: von der Ohe *et al.*, 2004; *hedgehogs*: Saboureau *et al.,* 1979; *humans*: Wehr 1998; *primates*: Rose *et al.*, 1978, Wilson *et al.*, 1978, Coe and Levine 1995, Sousa and Ziegler, 1998, Stavisky *et al.*, 2001b; *sand rats*: Amirat *et al.*, 1980; *fish*: de Pedro *et al.*, 1998, Fivizzani *et al.*, 1984; for review see Lane, 2006). Daily fluctuations in glucocorticoid production are widespread (e.g., Cavigelli *et al.*, 2005 [mice]; Fulkerson and Tang, 1979 [sheep]) and occur under control of the biological clock to help regulate metabolic activity (Dallman, 1993; Dallman *et al.*, 1993) and maintain homeostasis. Although age (Gust *et al.*, 2000) and social status (Cross and Rogers, 2004) may have additional effects upon diurnal patterns of cortisol secretion, the typical mammalian pattern of corticoid (corticosterone or cortisol) secretion, also seen in some non-mammalian species (e.g., sparrows: Breuner, *et al.*, 1999; Romero and Remage-Healey, 2000), consists of peak corticoid levels at or

just prior to first activity (Coe and Levine 1995; Czekala *et al.* 1984; Rusak 1989; Stavisky *et al.*, 2001b; Wilson *et al.*, 1978; Sousa and Ziegler, 1998; but see Fulkerson and Tang, 1979). Corticoid levels are highest in the morning in diurnal species and in the evening in nocturnal species, and peak levels are often coincident with the onset of locomotion. These daily elevations are not a result of activity, however, as these increases in corticoid levels appear to be cued by circadian clocks in the same way that activity patterns are maintained in species; a corticoid surge enables the mobilization of energy required for the demands of the active period (Nelson *et al.,* 2002). Subsequently, mammalian basal corticoid levels remain somewhat elevated throughout the day and gradually decline (Coe and Levine, 1995; Whitten *et al.*, 1998a), though they are subject to modification. Daily troughs in corticoid levels typically occur with the onset of inactivity and remain low until the pre-activity elevation.

Glucocorticoid levels may also fluctuate seasonally. Seasonal fluctuations in baseline cortisol levels are reportedly present in 70% of all species studied, and 88% of all mammals studied (Romero, 2002), and may be associated with transitory factors such as reproductive cycle and weight (Schiml *et al.*, 1996; Bales, 2005; French *et al.*, 2004; for review see Romero, 2002, Reeder and Kramer, 2005, and Keay *et al.*, 2006) or level of mate competition (Perret and Predine, 1984; Bercovitch, 1992; Strier *et al.,* 1999; Lynch *et al.,* 2002). While psychosocial stress has been studied extensively in vertebrates, the ecological correlates of cortisol secretion have received less attention, and the majority of what is known is based upon avian studies (*e.g.,* Astheimer *et al.,* 1995; Wingfield *et al.,* 1997; Romero and Remage-Healey, 2000; Rich and Romero, 2005; Buck *et al.,* 2007; Müller *et al.,* 2007; Schoech *et al.,* 2007).

The way in which cortisol levels respond to the physical environment as it presents a novel set of challenges throughout the year is relatively unknown. Regular seasonal environmental fluctuations may impact cortisol levels as energy stores are mobilized when energy in the environment becomes less available and/or more energy is needed for activities such as thermoregulation or acquiring food. Varying cortisol levels have been associated with seasonal changes in weather and resource distribution and availability in a variety of vertebrate taxa (Astheimer *et al.* 1995; Chapman *et al.,* 2006; Foley *et al.*, 2001; Huber *et al.*, 2003; Pride, 2005a; Strier *et al.* 1999). For instance, Huber *et al.* (2003) reported that red deer *(Cervus elaphus)* cortisol levels were significantly elevated in winter as a result of plummeting temperatures. In African elephants *(Loxodonta africana)*, rainfall is a limited resource, and conception rates are substantially higher during wetter years (70% vs. 9%). Foley and colleagues (2001) found that cortisol levels increased with seasonally declining water, body condition, and food.

Modifying factors and the flexibility of species may be investigated through population-level comparisons. Group size, climate, competition, territory size, the availability of food resources, tourism, and anthropogenic disturbance in general have all been associated with significant differences in corticoid levels among populations (Goymann *et al.,* 2001; Pride, 2005a; Lucas *et al.,* 2006; Walker *et al.,* 2006; Tarlow and Blumstein, 2007), indicating social and environmental factors which may alter or disrupt normal life histories. One interesting finding is that populations may differ in what they respond to as challenging. For instance, adult Megellanic penguins *(Spheniscus magellanicus)* in high-tourist areas had a weaker stress response to tourist presence than

those who lived in low-tourist areas (Walker *et al.,* 2006), demonstrating species' abilities to habituate to disturbance (see Romero, 2004). It appears that, as a stressor becomes more predictable or frequent, animals may adjust with a muted stress response. The impact of attenuation to one stressor may cause a heightened response in the context of other challenges (see Romero, 2004), suggesting that this relationship is complex and best investigated concurrently with several parameters.

The effects of habitat disturbance have also been investigated through comparing populations living in different sites, and in general populations with higher corticoid levels are assumed to be stressed (*e.g.,* Sayre, 1996; Creel *et al.,* 1997; Wasser *et al.,* 1997; Chapman *et al.,* 2007). For instance, Carolina chickadees *(Poecile carolinensis)* in a recently logged forest with lower body mass excreted higher mean corticoid levels than those in undisturbed forest (Lucas *et al.,* 2006). Inter-site comparisons of corticoid levels may also yield results indicating no difference between sites (red deer: Sauerwein *et al.,* 2004; blue tits: Müller *et al.,* 2007) as well as more stress in undisturbed forest (bighorn sheep: Sayre, 1996) (Table 4.1).

Cyr and Romero (2007) caution that the study of cortisol levels in wild mammals is still in its infancy, and it is too early to assume that populations with higher corticoids are always more stressed. Corticoids are secreted to help species cope with stressors, so elevations may indicate either successful coping or chronic stress. Similarly, low corticoid levels may indicate the absence of stress, tolerance ("the intensity of disturbance that an individual tolerates without responding in a specified way", Nisbet, 2000, p. 315), habituation, attenuation, or the complete cessation of the stress response (Homan *et al.,* 2003; Romero, 2004). Exposure to previous stressors must be considered

when interpreting such data. In a recent study designed to determine the impact of stress upon fitness, experimentally stressed European starlings *(Sturnus vulgaris)* had lower baseline and stress-induced corticoid levels than starlings unexposed to a stress regime (Rich and Romero, 2005; Cyr and Romero, 2007). Furthermore, starlings with lower baseline corticoids experienced lower reproductive success (Cyr and Romero, 2007). Before assuming that wild populations with elevated corticoid levels are stressed, the relationship between corticoid levels and stress must first be investigated in wild populations. Furthermore, if the predicted relationship between habitat disturbance and basal cortisol levels is largely dependent upon resource availability, broader investigation of taxa exploiting different dietary niches must occur.

Habitat disturbance may intensify the impact of natural seasonal fluctuations in climate and food availability upon species, but the majority of studies was not conducted throughout the year, and may have overlooked seasonal hormonal responses which are essential to understanding how animals cope with environmental challenges (see Romero, 2002). Detailed data on temporal heterogeneity in the environment such as monthly food availability further provides a context within which to interpret glucocorticoid variation. Comparing mean basal levels is informative, but elucidating the circumstances under which animals in different habitats mobilize energy, and how *these* compare, can inform on the flexibility of species, their energetic strategies, and mechanisms influencing reproductive success.

Table 4.1. Studies of cortisol comparing mammalian populations in disturbed and undisturbed sites. All studies extracted hormones from feces except where indicated.

Species	Site with Higher Corticoid[1,2] Levels	Duration	N Samples	N Individuals sampled in study	Reference
Chickadees[2]	Disturbed	9 months	87	77	Lucas *et al.,* 2006
Black Howler Monkeys[1]	Disturbed	8 months	72	____	Martinez-Mota *et al.,* 2007
Midday Gerbils	Disturbed	2 months	113	49	Kuznetsov *et al.,* 2004
Red Colobus[1]	Disturbed	Approx. 1 month	98	____	Chapman *et al.*, 2006
Red deer[3]	No difference	No duration	65	65	Sauerwein *et al.*, 2004[3]
Bighorn sheep[1]	Undisturbed	12 months	160	15	Sayre, 1996

[1] Studies measured cortisol.
[2] Studies measured corticosterone.
[3] Cortisol metabolites measured in ileal digesta in 7 different sites.

Primates and Stress

Primates may be particularly susceptible to reduced reproductive success from ecological and social pressures due to the slower life-history patterns characteristic of this Order. Primates generally produce relatively few offspring in a lifetime, who mature slowly and are dependent for an extended time (Charnov and Berrigan, 1993). Increased time and energetic requirements for reproduction and the survival of offspring relative to other mammals make this group particularly sensitive to physiological stress (Tilden and Oftedal, 1995). Reproductive strategies are ultimately determined by the ability of an individual to acquire enough food resources for itself and its offspring (see Tecot, Chapter 1). As environmental and social stressors can inhibit reproduction (Mendoza and

Mason, 1988; Sapolsky, 1992; Abbott *et al.,* 1998, 2003; Wingfield and Sapolsky, 2003), the lifetime reproductive success of primates impacted by these stressors may be reduced more severely than in other, faster reproducing mammals.

Primates, Unpredictability, and Cortisol

In general, investigations of the primate adrenocortical response have determined that unpredictability elicits cortisol level elevations. Captive female cotton-top tamarins *(Saguinus oedipus)* had higher urinary cortisol levels when moved into novel social environments than when housed in natal groups (Ziegler *et al.,* 1995), suggesting that unpredictable social conditions are stressful. Numerous studies of the hormonal correlates of dominance have met with varied results (Abbott *et al.,* 2003), where dominant individuals have either higher (Sapolsky, 1991) or lower (Chamove and Bowman, 1976; Kaplan, 1986; Sapolsky, 1983) cortisol levels, or there is no relationship between rank and cortisol levels at all (Sapolsky, 1983; Gust *et al.*, 1993). The stability of the hierarchy appears to be the best predictor of cortisol levels (Sapolsky, 1992). For instance, the alpha individual may have high cortisol levels in an unstable group where the unpredictability of becoming ousted and increased aggression may cause increased stress. The same individual may have low cortisol levels during group stability where aggression is infrequent and access to resources is relatively easy (Sapolsky, 1991).

Social structure can also predict adrenal activation because of this relationship between unpredictability and stress. For example, titi monkeys live in socially monogamous, territorial groups and had greater adrenal sensitivity to environmental novelty such as changes in sound, smell, or cage compared with squirrel monkeys which live in multi-male and female groups (Hennessy *et al.,* 1995). In titi monkeys a slight

change in novelty elicited cortisol level elevations and small incremental changes in novelty were reflected in cortisol levels. Conversely, considerable changes in novelty were required for an adrenal response in squirrel monkeys. Hennessy and colleagues (1995) suggest that the difference in adrenal sensitivity between these two species is due to the fact that titi monkeys experience novelty to a lesser degree in their social groups. For instance, while squirrel monkeys venture into new environments or take variable routes to reach resources, titi monkeys tend to remain within their familiar territories and live in groups in which membership is stable. Hence, titi monkeys may not be well adapted to a squirrel monkey lifestyle, but their sensitivity enables them to survive in and protect a known territory.

Primates and Seasonal Cortisol

Seasonal variations in cortisol levels have been associated with reproduction and psychosocial stress among primates. Where male competition for females is high, a pre-breeding increase in male body weight, which confers reproductive advantages over other males, is accompanied by cortisol level elevations (Perret and Predine, 1984; Wiebe *et al.,* 1988; Bercovitch, 1992; Schiml *et al.,* 1996). Even in species where male competition is low, pre-breeding increases in cortisol may be absent, but breeding season increases still occur (Lynch *et al.* 2002; Strier *et al.* 1999; Tecot, in preparation). In cooperatively breeding New World monkeys (da Silva Mota *et al.*, 2006; Ziegler *et al.*, 1996, 2004) and lemurs (Tecot, 2007b; Tecot, in preparation), females' basal cortisol levels increase mid-gestation and male elevations follow. This relationship may be associated with infant bonding (Nunes *et al.*, 2001; Storey *et al.*, 2000; Ziegler *et al.*,

2004), stimulating the release of other important parenting hormones necessary for infant care-giving behaviors (Fleming *et al.*, 2002; Ziegler, 2000).

The relationship between climate seasonality and primate cortisol levels remains understudied and unclear. In addition to the challenges wrought by temporal heterogeneity of food availability and quality, temperature fluctuations may severely energetically drain species (Hammond and Diamond, 1997). Primates commonly respond to temperature changes by modifying their behaviors (Pollack, 1979; Watts, 1988; Engqvist and Richard, 1991; Richard and Dewar, 1991; Morland, 1993; Overdorff and Rasmussen, 1995; Schmid and Ganzhorn, 1996; Powzyk, 1997; Nash, 1998; Curtis *et al.*, 1999; Estrada *et al.,* 1999; Pereira *et al.*, 1999; Wright, 1999; Vasey, 2005; Fernandez-Duque and Erkert, 2006; Tecot, Chapter 3). It has been suggested that only severe weather such as cyclones will influence the HPA axis since mild changes in climate are largely predictable (see Romero, 2002). Higher cortisol levels excreted during the cold season in chacma baboons (Weingrill *et al.,* 2004) suggest that this physiological response may help species avoid thermal stress associated with normal seasonal fluctuations.

Precipitation may similarly introduce thermoregulatory challenges. In contrast with other mammalian taxa (see above), muriqui male (Strier *et al.,* 1999) and Verreaux's sifaka (Fichtel *et al.,* 2007) cortisol levels were significantly elevated during the wet season, indicating that thermal stress may be exacerbated with precipitation. However, Fichtel *et al.* (2007) suggested that cortisol elevations in sifaka were due to the coincident reproductive season, and Strier *et al.* (1999) suggested that since precipitation was a good indicator of fruit availability, cortisol levels may have been responding to food resources

(see also Lynch *et al.,* 2002). Similar to African elephants (see above; Foley *et al.,* 2001), ringtailed lemurs living in highly seasonal habitats with extremely unpredictable and extended dry seasons experienced higher cortisol levels during the dry season (which, however, also coincided with tamarind abundance) (Pride, 2005a). More research is necessary to determine the influence of climate, mild or severe, on seasonal cortisol levels in primates.

Nutritional challenge has been associated with elevated primate cortisol levels and suggests that seasonal fluctuations in food availability might require energy mobilization, as seen in other vertebrate taxa. In captive squirrel monkeys, predictable, optional foraging tasks promoted psychological well-being, whereas unpredictable foraging demands chronically stressed monkeys, as indicated by prolonged, increased levels of cortisol (Champoux *et al.,* 1993). Similar results have been found in captive capuchins, where unpredictable feeding schedules elicited significantly higher levels of fecal cortisol (Ulyan, *et al.,* 2006), suggesting that unpredictable food availability may elicit higher cortisol levels in unpredictable environments, such as those where resources have been selectively extracted.

Studies on the impact of the natural environment on primate glucocorticoid levels are rare, but studies indicate that food scarcity in *seasonal* environments may also elicit cortisol elevations. Though seasonal environments are predictable to some extent, adrenal activation may be sustained where, for instance, resource scarcity is prolonged and/or supra-annually unpredictable. In the wild, high cortisol levels were found during the lean season in baboons (Sapolsky, 1986), chimpanzees (Müller and Wrangham, 2004), and ring-tailed lemurs (Cavigelli, 1999; also suggested in Pride, 2005a), and

higher cortisol levels were found in colobus monkeys in months which were preceded by the consumption of lower quality food (Chapman *et al.,* 2007). Although cortisol levels may not always track food availability in wild primate species, ecological challenge may be elucidated by making comparisons of populations exposed to different ecological matrices. For instance, *Lemur catta* in a drier and less predictable habitat excreted higher cortisol levels during food scarcity, yet those in a more predictable habitat did not (Cavigelli, 1999).

While results are equivocal for vertebrates in general, a few recent studies investigating the relationship between habitat quality and cortisol levels in primates found for the most part that more degraded forest elicited higher cortisol levels than intact forest, and concluded that disturbed habitats were more stressful than undisturbed habitats. Black howler monkeys (*Alouatta pigra)* living in forest fragments excreted higher mean cortisol levels than monkeys in continuous forest (Chapman *et al.,* 2006), suggesting that elevated cortisol may be a good indicator of a stressed population, and ultimately population decline. It is difficult to determine, however, whether such increases in cortisol were due to nutritional stress, increased activity, or some combination of the two, since *Alouatta sp.* also altered diet and range size in relation to fragment size (Bicca-Marques, 2003), and cortisol levels from two months were used to compare populations.

There is a large gap in our knowledge of the relationship between natural seasonal changes in the physical environment and the primate stress response. Few species have been studied in the wild where they are subject to the environmental pressures which have shaped their stress physiologies. Long-term studies spanning several seasons will

help identify sources of stress in the environment, and ultimately help answer evolutionary questions.

Lemur Stress: Models of Lemur Evolution

While primates as a group may be remarkably susceptible to reduced reproductive success from stress, lemurs in particular may be an interesting group on which to test the influence of environmental stress. Reproduction and ecology have played major roles in evolutionary models that propose reproductive or ecological stress as adaptive forces causing unique lemur behavior and physiology. Yet, activation of the lemur stress response has not been directly measured in association with both reproductive and environmental change.

Madagascar is distinct from other primate regions because of its climate and inter-annual unpredictability (Wright, 1999; Wright *et al.,* 2005; Wright, 2006; Dewar and Richard, 2007). Madagascar's climate is historically harsh and unpredictable, with frequent droughts, cyclones, and frosts (Ganzhorn, 1995a; Sauther, 1998; Ganzhorn *et al.,* 1999b; Wright, 1999). There is seasonal variation in rainfall and fruiting peaks, low soil fertility, slow tree growth, and small tree crown diameter, particularly in the eastern rainforests (Morland, 1991; Hemingway, 1995; Overdorff, 1993a, 1996a; Overdorff and Strait, 1998; Ganzhorn *et al.,* 1999ab; Hemingway and Overdorff, 1999; Wright, 1999; Wright *et al.,* 2005; Dewar and Richard, 2007). Fruit is unavailable up to six months each year, approximately three months longer than in other primate habitats (Wright, 1999; Wright *et al.,* 2005). Additionally, cyclones frequently kill immature trees and inhibit fruiting, further reducing the predictability of resource availability (Hemingway, 1995; Wright, 1995; Sauther, 1998).

Madagascar's environment is hypothesized to have strongly influenced lemur evolution (Smith and Ganzhorn, 1996; Wright, 1999; Dewar and Richard, 2007). Lemurs as a group possess many unique traits compared with other primates, such as cathemerality (polyphasic activity pattern throughout a 24-hour cycle; Tattersalll, 1987), synchronized breeding with very short estrus periods and a narrow breeding season ("a discrete period of the year to which all births are confined" Lancaster and Lee, 1965, p. 488), low basal metabolic rate (Kurland and Pearson, 1986; Snodgrass *et al.,* 2007), and monomorphy (Jolly, 1966; Wright, 1999). Historically researchers hypothesized that these traits were the result of reproductive stress (Jolly, 1984; Richard and Nicoll, 1987; Richard and Dewar, 1991). Young *et al.* (1990) postulated that lemur females undergo high energetic burden during reproduction (gestation and lactation) relative to energy available in the environment. However, in comparison with other primates, postnatal reproduction in lemurs is not particularly energetically expensive (Kappeler, 1996; but see Godfrey *et al.* 2004), and more recent studies attribute these traits primarily to adaptation to environmental or nutritional stress (Tilden and Oftedal, 1995; Kappeler, 1996; Wright, 1999); through adaptation to Madagascar's environment, lemur traits may help lemurs *avoid* extreme reproductive and ecological stress (Tilden and Oftedal, 1995; Pereira *et al.,* 1999).

Wright's (1999) energy frugality hypothesis (EFH) proposes that the harsh, unpredictable environment in which lemurs live contrasts with other primate habitats, and this environment selected for the evolution of unique traits, which conserve energy (Jolly, 1984), and maximize food resources (Table 4.2). For instance, small group sizes may be an energy conservation strategy that allows scarce resources in small tree crowns to last

longer (Ganzhorn *et al.,* 1999a) and reduces competition within the group (Wright, 1995, 1999). Red-bellied lemurs *(Eulemur rubriventer*) living in small family groups fed for longer periods of time per resource than rufous lemurs *(Eulemur fulvus rufus)* living in large multi-male multi-female groups (Overdorff, 1993). Cathemerality may be a resource maximization strategy providing temporal flexibility in foraging, optimizing the exploitation of food resources during times of greatest abundance and quality, and low predation risk (Rasmussen, 1999). Thus, rather than adaptations reflecting stress associated with severe energy deficits, these unusual traits help lemurs avoid chronic stress, maximizing present resources to survive periods when resources are severely limited, and are specially suited to avoid the adverse effects of Madagascar's environment. Thus, it is proposed that lemurs are not more stressed than other mammals, and periods of abundance may be critical in helping lemurs avoid chronic stress during periods of scarcity (Pereira *et al.,* 1999).

For instance, nutrient storage and growth during the abundant season may help lemurs avoid nutritional stress during the scarce season. There is a strong response to photoperiod in captive lemurs (van Horn, 1979; Rasmussen, 1985; Pereira *et al.,* 1993) such that certain adjustments made in captivity correspond to particular seasons in the wild. Pereira and colleagues (1999) report that during times of the year when temperatures are low and food is scarce, *Eulemur fulvus rufus* and *Lemur catta* activity and appetite decrease (such that they decline food), growth rates of hair and juveniles decrease, and high levels of metabolic hormones indicate energy extraction from adipose tissue. This period also corresponds to gestation for those species. Conversely, when temperatures are warmer and food is abundant, time spent feeding increases to a point

where 100% of provisioned food is eaten, hair and juvenile growth rates increase, and metabolic hormones decrease indicating energy storage as adipose tissue. However, in the eastern rain forests of Madagascar, although frugivorous species such as *Eulemur rubriventer* and *Varecia variegata* become less active when food is declining, they also *increase* time spent feeding (Overdorff, 1993a; Morland, 1993; Tecot, Chapter 3). In the absence of phytochemical analyses or physiological measures, it is unclear, however, whether this strategy is due to seasonal differences in the nutrient content of food (*e.g.,* animals feed longer on lower quality resources), and if animals are able to store nutrients in the absence of increased time feeding during fruit abundance. This is an intriguing question, as reduced resting metabolic rates and fat storage combined extend the period during which animals of relatively small size may endure seasonal resource sinks (Humphries *et al.,* 2004).

Lemurs can be quite flexible, however, and their behavior is subject to modifying factors. For instance, the unique lemur traits associated with reproduction can vary in response to the environment, and may help alleviate stress. Several researchers have reported wide birth peaks lasting as long as 3 months (*e.g.,* Budnitz and Dainis, 1975; see also Whitten and Brockman, 2001; Brockman and van Schaik, 2005; Tecot and Overdorff, 2005), inter-annually aseasonal breeding where births occur in several different months from year to year (*e.g.,* Mutschler, 1999; Tecot and Overdorff, 2005; for a review see Brockman and van Schaik, 2005 and Whitten and Brockman, 2001), and births occurring more often than once per year (Tecot and Overdorff, 2005). The source and extent of this flexibility is unknown, and is suggested to be directly related in part to the physical environment (Whitten and Brockman, 2001). Malagasy Lemurids and

Indriids may employ different growth and reproductive strategies based upon their different diets (Godfrey *et al.,* 2004), and the availability of food most likely does have an effect on reproductive behavior. As a group, Madagascar's primate species may differ substantially from other primates because of Madagascar's specific environmental stressors (Wright, 1999; Godfrey *et al.,* 2004).

Table 4.2. Proposed energy conservation and scarce resource maximization traits observed in Lemurids. Based upon the Energy Frugality Hypothesis (Wright, 1999).

Energy Conservation	Scarce Resource Maximization
Small Group Sizes	**Cathemerality**
Torpor	**Territoriality**
Sperm Competition	**Female Dominance**
Low Basal Metabolic Rate	**Fibrous Diet**
Seasonal Breeding	**Weaning Synchrony**

Anthropogenic disturbances have also shaped Madagascar's unique environment, introducing an additional component to the unpredictability of the resource base. Madagascar has some of the richest primate species diversity, but has suffered a 90% loss of habitat mainly due to logging and agricultural clearing over the past 2000 years, since humans arrived on the island, and which has also been met with extensive extinction (MacPhee and Burney, 1991; Nelson and Horning, 1993; Mittermeier *et al.,* 2006). In conjunction with Madagascar's particular climate, anthropogenic disturbances yield fragmented forests with intensified periods of scarce and unpredictable resource availability. Habitat loss often translates to a loss of habitat diversity and more specifically fruit diversity, which can further intensify the effect of the lean season (Terborgh, 1986b). Furthermore, the particular forests that lemurs inhabit are among the

most threatened forests in the country (Green and Sussman, 1990). Lemurs in heavily disturbed areas are the most vulnerable to climatic disturbances because forest fragmentation prevents them from dispersing to larger forests (Ganzhorn *et al.,* 1996/7, 1997; Wright, 1999) and induces crowding, intensifying the effects of scarce resources.

Habitat alteration affects the density and distribution of many lemur species (Harcourt and Thornback, 1990; Dagosto, 1989; White *et al.,* 1995; Johnson and Overdorff, 1999; Grassi, 2001; Irwin, 2006), and intraspecific variation in lemur behavior is evident as a result of the differential resource distribution and abundance caused by forest fragmentation (Harcourt and Thornback, 1990; White *et al.,* 1995; Porter, 1998; Grassi, 2001; Tecot, Chapter 3). Several studies of conspecifics in Madagascar have investigated the behavioral and demographic correlates of habitat composition, and found differences in locomotion style, feeding preference, population density, and group size (Dagosto, 1989; White *et al.,* 1995; Johnson and Overdorff, 1999; Balko, 1998; Nash, 1999; Grassi, 2001). In lower quality habitats some species exist in larger groups and higher densities, while others decrease in size and density. While these studies demonstrate inter-site diversity and behavioral flexibility, they also indicate that population density and other measures *alone* are not reliable indicators of stress, nor are they sufficient to indicate fitness risk associated with habitat quality (Hofer and East, 1998; Merenlender *et al.,* 1998).

To determine how lemurs respond to ecological stress in rain forest environments, it is critical to investigate the proximate mechanisms mediating these behaviors. Hormonal studies are the next critical step that must be taken in the field of socioecology to identify which external pressures influence Lemurids and how these pressures impact

their energetic strategies. Determining the physiological response to seasonal changes can help identify regular periods of challenge and determine the physiological response to unpredictability by comparing such disturbed habitats with those left relatively untouched.

Lemurid Hormone Studies

There have been few studies employing hormonal measures in the study of wild Malagasy primates (*e.g., Propithecus verreauxi:* Brockman, 1994, Brockman and Whitten, 1996, Brockman *et al.,* 1998, Kraus *et al.,* 1999, Fichtel *et al.,* 2007; *Lemur catta:* Cavigelli, 1999; Cavigelli *et al.,* 2003, Gould *et al.,* 2005; Pride, 2005ab; *Eulemur fulvus rufus:* Ostner *et al.,* 2002). Furthermore, few of these studies measured cortisol levels, one in *Propithecus verreauxi* (Fichtel *et al.,* 2007; see also Brockman *et al.,* 2000, 2003), and the remainder in *Lemur catta* (Cavigelli, 1999; Cavigelli *et al.,* 2003; Gould *et al.,* 2005; Pride, 2005ab). These studies have been increasingly illuminating, as they indicate that lemurs may respond to their social environments differently than other primates. For example, Gould and colleagues (2005) determined that male *Lemur catta* cortisol levels did not significantly differ between mating and non-mating seasons, in contrast with studies of other primates with significant mating season competition among males (*e.g.,* Wiebe 1988 (captive *Saimiri boliviensis boliviensis*); Perret and Predine, 1984 (captive *Microcebus murinus*)). However, dominant female *Lemur catta* (Gould *et al.,* 2005) and male *Propithecus verreauxi* (Fichtel *et al.,* 2007) resemble anthropoid primates who show relatively higher cortisol levels than subordinates during periods of increased aggression (see Abbott *et al.,* 2003). As studies of lemurid cortisol are just

beginning, the hormonal response of these species to the physical environment remains unexplored.

Temperature is proposed to be of critical importance to seasonally changing physiology and behavior in lemurs (Morland, 1993), yet studies of the physiological correlates to temperature variations are lacking. As mentioned above, two studies reported a relationship between precipitation and lemur cortisol levels, and none have investigated the impact of temperature change (Pride, 2005a; Fichtel *et al.,* 2007). While two studies are not sufficient to determine a general pattern, conflicting results from these two studies suggest that the relationship between precipitation and cortisol levels may be dependent upon the length and severity of the dry season, and the interaction with fruit availability and reproductive stage. For instance, where the dry season is extended and severe, *Lemur catta* cortisol levels are negatively associated with rainfall, which was also coincident with the fruiting of preferred resources (Pride, 2005a). Although Fichtel *et al.* (2007) did not test the effect of precipitation on sifaka cortisol levels directly, they report a positive relationship between rainfall and cortisol levels in a dry deciduous forest, and suggest that reproductive stage may be responsible for this effect of rainfall on cortisol levels.

Early studies of lemurs' responses to food availability are also equivocal. Similar to other primates, periods of food scarcity (Pride, 2005a) and times of greatest feeding effort (Cavigelli, 1999) were coincident with high cortisol levels, indicating metabolic stress. In contrast, Cavigelli (1999) found that cortisol levels did *not* change seasonally with food availability in all groups; only those individuals inhabiting a relatively harsher habitat responded to food scarcity (Cavigelli, 1999).

While these studies investigated the relationship between food availability and cortisol levels, the field of lemur stress ecology remains largely unknown. The next essential steps that must be taken involve broader and more detailed longitudinal analyses. Firstly, longitudinal studies are essential to document how species respond to environmental change, particularly when studying species in different habitats, where changes in climate, reproduction, and/or resources may not occur synchronously. Furthermore, the ability to cope with current challenges may depend in part upon the state of the environment several months prior.

Secondly, to begin an assessment of how the environment might exert selective pressure upon lemur species, detailed ecological assessments must be made. For instance, frugivorous species may respond to the availability of preferred fruit resources (Pride, 2005a), but other items such as flowers may be just as important to a frugivore (Pereira *et al.,* 1999), particularly during fruit scarcity. Furthermore, some lemur species exploit over 100 species for a variety of foods (*e.g., Eulemur rubriventer*, Overdorff, 1991; Tecot, this study) and a full analysis of food availability would ensure consideration of all nutrients incorporated into the diet as energy.

Thirdly, food availability seasons are often synchronized with specific reproductive stages, and it may be difficult to separate the effects of resource decline and reproduction. Similarly, dominance interactions may be associated with food availability, and in turn affect cortisol levels. Analyses of more lemur species with different reproductive schedules, or conspecific populations with access to different resources, will help disentangle these relationships.

Fourthly, as lemurs are endangered and field endocrinology is relatively novel, the hormonal profiles of few lemur species in the wild have been examined, and what we know of lemur stress ecology is limited to two species. Lemurs are unique, but they are also diverse. Extending such studies to species in different habitat types, with different social and mating structures, life histories, and even group sizes (see Pride, 2005a) will provide enormous comparative power with which to test evolutionary models of lemur evolution.

Finally, a comprehensive model requires a coordinated analysis of phenological and time budget data to clearly discern what energetic strategies are employed (Cavigelli, 1999). For instance, during the lean season animals may delay increasing glucocorticoids until conditions become severe, they may increase glucocorticoids throughout the season in short bursts, or they may increase glucocorticoid levels immediately upon experiencing a food decline (see Cavigelli, 1999). Species may even down-regulate glucocorticoid excretion in the face of acute stress if it occurs during a key life history stage (Wingfield and Romero, 2001). Behavioral modifications, too, may take on several different forms. For example, time spent feeding may increase to compensate during the onset of the scarce season; feeding time may increase initially and later decrease as glucocorticoids are excreted; or feeding times may remain low (*e.g.,* Pereira *et al.,* 1999; Curtis, 2004). Determining which strategies of energy intake, mobilization, and conservation are employed is essential to understanding what environmental parameters are exerting selective pressure, how severely populations are stressed, how resilient animals are, and what factors shape these strategies.

Noninvasive Measures of Cortisol

Interest in the study of stress in wild animals has increased substantially with the refinement and validation of techniques that can be used in the field. While serum cortisol is an excellent measure of stress and some researchers have been able to collect samples successfully in the wild (Sapolsky, 1982, 1993; Cook *et al.*, 2000), such techniques are not always practical in field situations. Stressors in the natural habitat can be investigated using methodological advances in cortisol acquisition, such as extraction from feces and urine (Risler *et al.,* 1987; Gross, 1991; Miller *et al.,* 1991; Monfort *et al.,* 1997; Whitten, *et al.,* 1998ab; Cavigelli, 1999; Stavisky *et al.*, 2001a). Despite concerns over the difficulty in collecting fecal and urine samples appropriate for analysis (e.g., Sauerwein *et al.*, 2004), and extensive methodological considerations (Möstl and Palme, 2002; Touma and Palme, 2005; Lane, 2006), researchers have been able to reliably collect, extract, and measure cortisol metabolites in feces and urine in a wide variety of vertebrate species, including primates (Wasser *et al.,* 2000). Administration of an "adrenocorticotropic hormone (ACTH) challenge" causes a stress response characterized by an acute elevation in circulating glucocorticoids. Experimental studies comparing serum and fecal glucocorticoid responses to ACTH challenge found that fecal glucocorticoid profiles (elevation and subsequent return to baseline levels) paralleled serum cortisol profiles, and concluded that fecal cortisol can reliably measure adrenal axis activity (e.g., Whitten *et al.*, 1998ab; Palme *et al.*, 1999; Terio *et al.*, 1999; Wasser *et al.,* 2000; Harper and Austad, 2002).

Fecal cortisol is advantageous because it allows the investigation of stressors in the natural habitat that may have an evolutionary impact on species, and eliminates the

additional stress associated with capture and venipuncture that may confound results (Dettmer *et al.,* 1996; Bronson, 1999). Fecal steroid analysis is also beneficial because it represents the accumulation of adrenal activation throughout one day (Sayre, 1996). This quality facilitates a more precise assessment of the impact of long-term processes compared with point sampling (Harper and Austad, 2000), and provides the best opportunity to examine the adrenal activity of species adopting different activity patterns such as cathemerality (day-night active: Tattersalll, 1987). Fecal extractions enable long-term sampling which can account for daily fluctuations, highlight prolonged influences upon an animal's physiology, identify patterns of stress sensitivity in response to seasonal changes, and ultimately identify selection pressures which affect the Darwinian fitness of species.

Eulemur rubriventer

This study examines *Eulemur rubriventer,* the red-bellied lemur, to analyze seasonal fecal cortisol levels and the effects of habitat differences on seasonal cortisol levels. *E. rubriventer* is an excellent species for this study for several reasons. First, monomorphy (Kappeler, 1991) eliminates the introduction of confounding metabolic- or other size-associated factors (Clutton-Brock *et al.*, 1977; Strier, 1987; Vasey, 2005) that may impact males and females differently. Second, *E. rubriventer* subsist mainly upon fruit (Overdorff, 1993ab; Tecot, 2007a), a resource which is patchy in time and space, thus facilitating a full analysis of the effects of resource seasonality. A frugivorous diet is also commonly associated with high sensitivity to habitat modification (Johns and Skorupa, 1987; Marsh *et al.,* 1987; Richard and Sussman, 1987; Struhsaker, 1997; Harcourt, 1998), so site differences are also best observed in a frugivorous species.

Third, *E. rubriventer* alter behavior in response to seasonal changes in food availability (Overdorff, 1988, 1996a; Tecot, Chapter 3), but in a divergent pattern from what would be predicted for energy storage (see Pereira *et al.,* 1999), and from what has been seen in several other species who increase feeding with food abundance (*e.g., Eulemur mongoz,* Curtis, 2004). However, exceptions to this pattern exist in this species (Tecot, Chapter 3) and provide the opportunity to investigate the physiological and environmental correlates of these variable relationships. Fourth, they live in small, territorial, strictly pair-bonded family groups (Merenlender, 1993; Overdorff and Tecot, 2006), and as a result may be more sensitive to environmental stressors compared with other primate species living in different societies (Hennessy *et al.*, 1995). Fifth, although most frugivorous species distinguish themselves from folivorous species by remaining active for the majority of the day, red-bellied lemurs display an odd combination of frugivory and extensive bouts of sleeping throughout the day (Overdorff, 1988; Tecot, Chapter 3). As resting increases with fruit abundance and decreases with folivory and fruit scarcity in this species (Tecot, Chapter 3), such a behavioral strategy may not be related solely to the digestive restrictions of the diet, but may also be related to energy storage for the lean season when time resting is limited by time spent foraging. Physiological measures can identify which strategies of energy accumulation, conservation, and expenditure are used by this species.

Hypotheses and Predictions

Three main sources of ecological stress are proposed for primates: fluctuations in climate, food availability, and the combined effect of these parameters as they interact with habitat quality. Based upon the relationship between seasonality and metabolic stress found in a variety of vertebrate taxa, and previously observed patterns in primates,

this longitudinal study examines how cortisol varies with climate, food availability, and habitat quality to identify potential environmental stressors. Behavioral data are examined with fecal cortisol levels overall and seasonally to determine how these mechanisms (behavioral, physiological, or both) are used to cope with energetic challenge. The following non-mutually exclusive hypotheses and predictions were made using *Eulemur rubriventer* as a model, studying populations in two sites: Talatakely (disturbed) and Vatoharanana (undisturbed) (see below for site details).

Hypothesis 1. Cortisol excretion will reflect challenge and fluctuate. During this study, energy available in the environment fluctuated with the thermal environment and food availability (Tecot, Chapter 2). Consequently, the proportion of time in which *Eulemur rubriventer* engaged in different behaviors varied throughout the year (Tecot, Chapter 3). If behavioral coping strategies are sufficient mechanisms to remain in energetic balance (*cf* Morland, 1993), fecal cortisol levels will not vary. However, if Madagascar's environment is particularly harsh, necessitating energy storage and extraction strategies to physiologically cope, fecal cortisol levels are expected to fluctuate.

Hypothesis 2. Seasonal patterns of temperature and precipitation will be reflected in annual patterns of cortisol. Mammalian cortisol levels may rise significantly in winter during coldest temperatures (Huber *et al.,* 2003; Weingrill *et al.,* 2004), and time resting may increase with cooler temperatures to mediate cold stress (Weingrill *et al.,* 2004). *Eulemur rubriventer* increase time resting during the cool season (Tecot, Chapter 3), and are similarly predicted to have higher cortisol levels during this time of year.

Since *Eulemur rubriventer* live in a tropical rainforest where water is not limited, and precipitation has been associated with increased energy expenditure (more feeding and less resting) (Tecot, Chapter 3), it is predicted that the wet season will be accompanied by higher cortisol levels as it presents a thermoregulatory challenge.

Hypothesis 3. Seasonal patterns of food abundance will be reflected in annual patterns of cortisol excretion. If the lean season poses a significant challenge, whether due to unpredictability in timing or the availability of energy, it may require substantial physiological modifications such as the extraction of stored energy (*e.g.,* Knott, 1998; Ulyan *et al.,* 2006), requiring both behavioral modifications and significant physiological modifications. It is thus predicted that peaks in cortisol levels will occur during periods of low food availability and troughs will occur during periods of high food availability.

Hypothesis 4. Habitat quality will be reflected in cortisol excretion, and energetic strategies will differ among sites. If anthropogenic disturbances create more unpredictable environments (see Tecot, Chapter 2), different strategies will be employed at each site. Resource availability differed greatly between the disturbed and undisturbed sites: in the disturbed site, preferred fruiting trees were productive for shorter lengths of time and food scarcity was prolonged and less predictable (Tecot, Chapter 2). Overall and seasonal patterns of cortisol excretion are expected to be similar in adjacent disturbed and undisturbed habitats, but sites are predicted to differ significantly in the magnitude, duration and timing of fecal cortisol elevations.

Patterns: Monthly and seasonal fluctuations in cortisol excretion will be similar in each site. Both populations are predicted to excrete higher cortisol levels during the cool and wet months (Hypothesis 2), and fruit scarce months (Hypothesis 3).

Timing: Since sites differed in the extent and timing of phenological cycling (Tecot, Chapter 2), monthly cortisol excretion is predicted to differ significantly among sites. Furthermore, cortisol increases are predicted to occur at the height of food scarcity in the disturbed site, and at the beginning of food scarcity in the undisturbed site.

Magnitude: The disturbed forest population is expected to experience more severe stress during energetically demanding periods. In the disturbed habitat, all relationships between cortisol excretion and season are predicted to be stronger, with a greater change in cortisol excretion between low-challenge and high-challenge seasons. During cool, wet, and fruit scarcity seasons (energetically demanding periods), fecal cortisol levels are predicted to be significantly higher in the disturbed habitat than in the undisturbed habitat.

Duration: If cortisol levels peak with low resource periods and these periods are prolonged in the disturbed habitat (Tecot, unpublished data), adrenal activation will be sustained. It is thus predicted that changes from baseline during low resource periods (Hypothesis 3) will be longer in duration in lower quality habitat populations.

Hypothesis 5: Seasonal patterns of activity will be reflected in annual patterns of cortisol excretion. Cortisol levels are predicted to co-vary with behavior if both physiological and behavioral mechanisms of coping are employed. The relationship between behavior and cortisol levels will be influenced by climate and food availability such that these relationships will be weaker during the seasons when cortisol levels are

lowest (*i.e.,* when energy requirements are lower). Stronger associations when cortisol levels are highest are predicted if both behavioral and physiological mechanisms help this species cope with energetic challenge. No significant differences between sites are predicted in the relationship between behavior and fecal cortisol levels.

Alternatively, phenology will be a better predictor of fecal cortisol levels than feeding, reflecting periods of energy storage and extreme stress. Since feeding and phenology were related and the proportion of time spent feeding increased when food was scarce (Tecot, Chapter 3), feeding and fecal cortisol levels were predicted to be correlated. However, since the relationship between feeding and phenology was not consistent every month, feeding time is not predicted to be significantly predictive of cortisol levels. Fecal cortisol levels are predicted to be low when increased time feeding occurs with food abundance (indicating energy storage), and high when decreased time feeding occurs with food scarcity (indicating stress). No significant differences between sites are predicted since these positive relationships between feeding and phenology occurred in both sites.

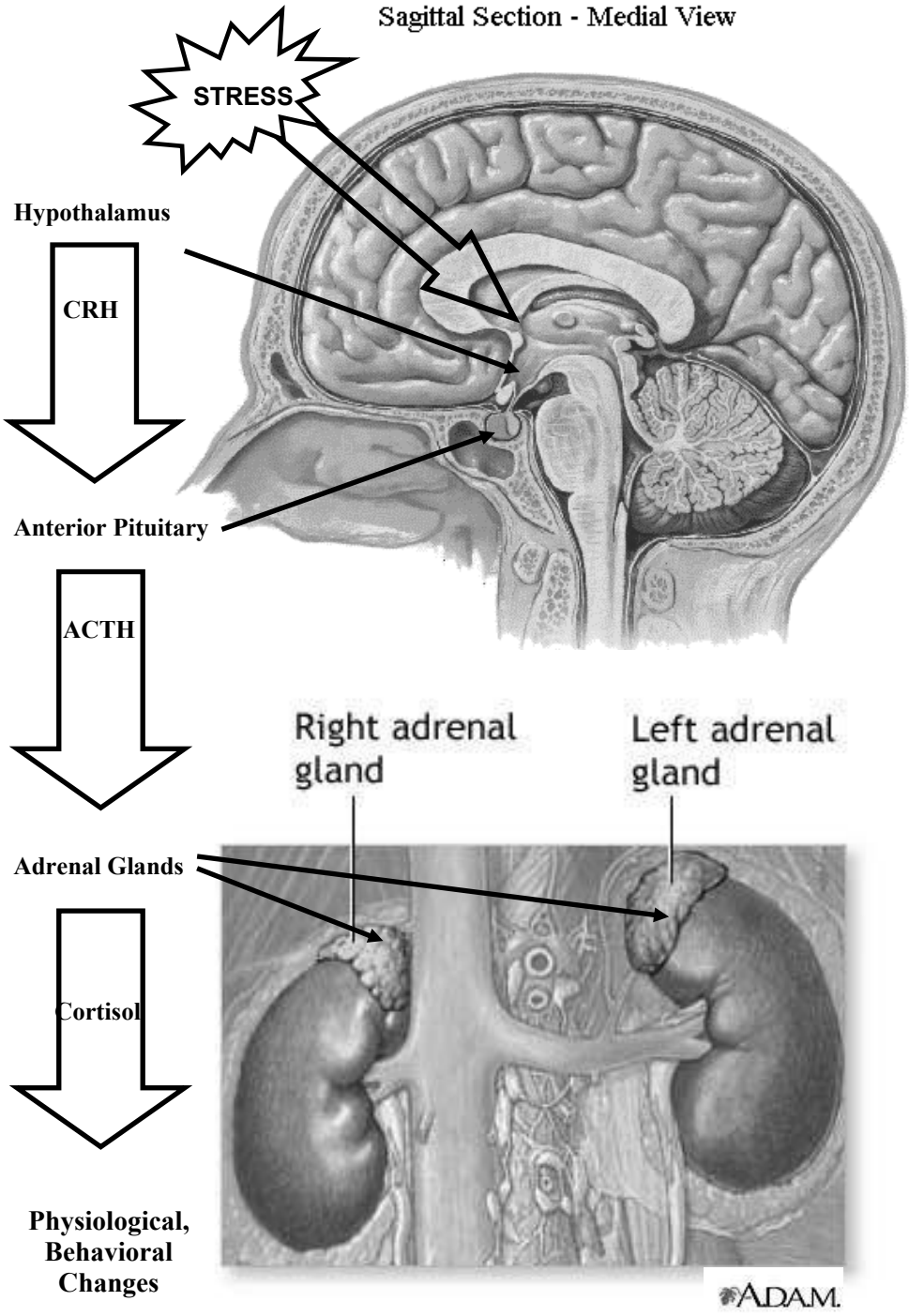


Figure 4.1. Hypothalamic-Pituitary-Adrenal Axis and the Stress Response. When a stressor is perceived the hypothalamus is stimulated to secrete corticotropin releasing hormone (CRH) which stimulates the anterior pituitary to secrete adrenocorticotropic hormone (ACTH). ACTH stimulates the adrenal cortex on the kidneys to secrete glucocorticoids such as cortisol. This initiates a cascade of physiological and behavioral adjustments. Brain image from Furman.edu; Adrenal image from A.D.A.M., Inc.

METHODS

To determine the relationships between climate, food availability, habitat, behavior and cortisol levels, this study examined five *Eulemur rubriventer* (red-bellied lemur) groups in Ranomafana National Park, Madagascar. Two groups were studied in a high-altitude primary rain forest (Vatoharanana), and three groups were studied in a low-altitude secondary rain forest (Talatakely). Data were collected January 2004-March 2005 (n = 2586 hours).

Sites

Ranomafana National Park (RNP) consists of approximately 43,500 ha of evergreen rain forest in Fianarantsoa Province, southeast Madagascar (between 21˚02' to 21˚25' S and 47˚18' to 47˚37' E) (DuPuy and Moat, 1995). This park contains the largest known population of *Eulemur rubriventer* (Wright 1992), as well as at least 11 other primate taxa (Wright, 1992). RNP ranges from lowland forest (500m) to montane rain forest (1500 m) and is highly seasonal with large peaks and prolonged troughs in food availability, particularly fruit (Hemingway, 1995; Morland, 1991; Overdorff, 1993a, 1996a; Overdorff and Strait, 1998; Tecot, Chapter 2). The amount of precipitation (avg. 1500 mm – 4000 mm per year) and the lengths of wet and dry seasons display extreme inter-annual variability (Overdorff and Wright, unpublished data; Wright, 1992; Wright, 2006). Cyclone activity typically occurs January through March. Phenological patterns are highly unpredictable from year to year, with the availability of fruits, flowers, and new leaves varying dramatically (Wright, 1999; Overdorff and Wright, unpublished data).

Within RNP, data were collected in two adjacent study sites, Talatakely and Vatoharanana, each with an established and maintained trail system (White *et al.*, 1995, Wright, 1997). The density and abundance of plant species (including those resources preferred by the lemur population) differ between these sites (Tecot, Chapter 2) as a result of selective logging (Turk, 1995; Wright, 1995; Balko, 1998).

Talatakely: Located near the park entrance at 500m in altitude, this site was heavily logged from 1986 to 1989 and is currently regenerating. As a result of habitat alteration, this site is characterized by secondary rain forest with large stands of Chinese guava (*Psidium* spp.), emergent *Eucalyptus* trees (Overdorff, 1988), a discontinuous tree canopy, lower tree species diversity, and trees smaller in diameter at breast height (dbh), height, and crown volume than those in Vatoharanana (White *et al.*, 1995; Balko, 1998; Tecot, Chapter 2). The understory largely consists of Rubiaceae and Myrsinaceae, bamboo, and epiphytic species (Turk, 1995). Research at this site was conducted within the 5 km^2 trail system.

Vatoharanana: This site is located 6 kilometers south of Talatakely, at approximately 1200m in altitude. Although this site was selectively logged and approximately 1,000 trees were removed (Balko, 1998), it is characterized by continuous primary forest with steep mountain slopes, higher productivity, greater tree diversity, a more continuous canopy, and trees larger in diameter at breast height, height, and crown volume than those in Talatakely (Balko, 1998; Overdorff, 1988; White *et al.*, 1995; Tecot, Chapter 2). Fruiting trees here are also more seasonal than those in Talatakely (Tecot, Chapter 2), and this site contains some tree species exploited by *Eulemur rubriventer* which are not present in Talatakely (Tecot, Chapter 2). Research at this site

was conducted within the 6 km^2 trail system, as well as an extended trail system constructed during this study and previously by S. Karpanty.

These sites are ideal for this study because they have experienced varying levels of habitat disturbance and, despite altitudinal differences, they are subject to similar climates (precipitation and temperature), facilitating inter-site comparisons without the potentially confounding influence of climatic differences.

Subjects

Eulemur rubriventer adults weigh approximately 1.55-2.21 kg (Tecot, unpublished data; see also Glander *et al.,* 1992; Terranova and Coffman, 1997). The diet of *E. rubriventer* is composed mainly of fruits and leaves, and supplemented with flowers, nectar, fungus, bark, dirt, and insects (Overdorff, 1988, 1991, 1993ab, 1996ab; Overdorff and Tecot, 2006; Tecot, 2006; Tecot, 2007a). Within Ranomafana National Park, *E. rubriventer* groups range in both disturbed and undisturbed forests, and ranges are approximately 12-15 ha (Overdorff, 1988). Densities within the park have been estimated to be anywhere from 5 to 19 individuals per km^2 (Overdorff, 1991; Grassi, 2001; Irwin *et al.*, 2005). Mating occurs between May and June, and births occur between September and October (gestation is approximately 120 days) (Overdorff, 1991), though out of season births have been documented (Tecot and Overdorff, 2005).

This study analyzes hormonal data collected from adults (n=12) in five groups (n_{Vato}=2 groups; n_{Tala}=3 groups) of *E. rubriventer* (Table 4.3). Individuals were identified by distinctive sexually dichromatic markings such as patches of white skin under the eyes of males or a white ventrum on females, or colored collars with tags.

Table 4.3. Group Compositions. Demography for groups in Vatoharanana (groups 1 and 2) and Talatakely (groups 3-5) throughout the 19-month study.

Group ID	# adult females	# adult males	# infants and juveniles	# immigrations (adults)	# emigrations	# deaths	# fecal samples
1	1	1	3	0	0	1	266
2	1	1	2	0	0	0	191
3	1	1	1	1	1[1]	1[1]	139
4	1	1	2	0	1	2	148
5	1	1	3	1	1	2	178
Total	5	5	11	2	2-3	4-5	922

[1] Emigrated or died.

Hormone Collection

Cortisol comparisons were conducted within and between individuals and groups, within and between sites. To determine the influence of habitat on the fecal cortisol levels of *Eulemur rubriventer* overall and seasonally, samples were collected from each site simultaneously over the course of nineteen months (between September 2003 and March 2005). Habituated groups from each site were followed daily for 5-day periods each week by teams of two to three observers. Fecal samples were collected between 0700 and 1200 to control for any circadian effect on cortisol excretion (Tecot, in preparation), with collection hours at each site divided between the focal groups each day when possible.

Fresh, whole, uncontaminated (by urine or stream water) fecal samples were collected from focal individuals immediately upon voiding, placed in aluminum foil, labeled with location, time, date, and individual identification, flattened to increase surface area, and dried by a fire or in an oven at 70º C for hormone preservation within 4

hours of collection (Brockman, 1994; Brockman and Whitten, 1996; Tecot, 2001). Samples were weighed on a scale before and after baking to establish water content. Dried samples were stored in Whirl-pak bags (Nasco, Fort Atkinson, WI) and combined in a freezer bag with desiccants. Attempts were made to collect at least one sample per individual per week by means of focal animal sampling (Altmann, 1974; Tecot, 2001). One to two samples per adult per week were typically collected, following Strier *et al.* (1999). Occasionally not all individuals were sampled in a week, but samples were collected from at least one individual per group each week. Because samples collected early in the study were from unhabituated individuals, only samples collected in November 2003 and later were assayed, for a total of 922 samples collected over the course of 74 weeks (17 months).

After the field season, samples were taken to the Wisconsin National Primate Research Center and assayed by the author, in collaboration with T. Ziegler and D. Wittwer. All samples were ground with a mortar and pestle and sifted through wire mesh to remove seeds and debris. Drying samples through both techniques resulted in a high recovery and stability (Tecot, 2001).

Hormone Extractions

Hormones were extracted from all fecal samples (n = 922). 0.10 g of dried feces from each sample was extracted into an ethanol-water (50:50) solution in 7.0 ml scintillation vials following Strier and Ziegler (1997). Using dried feces avoided any influence of diet upon cortisol excretion results (Wasser *et al.,* 1993). Samples were vortexed for 10 minutes and centrifuged for 10 minutes at 3000 rpm and the 5.0 ml supernatant poured off. In order to free conjugated steroids, 1.0 ml of each 5.0 ml

extraction was separated and 4.0 ml of solvent (ethyl acetate) were added. After each sample was again vortexed for 8 minutes and centrifuged for 3 minutes at 1000 rpm, the solvent was aspirated into culture tubes, evaporated in a water bath, and then resuspended in 1.0 ml 30% methanol. Samples were further purified through solid-phase extraction (SPE) columns (Ziegler and Wittwer, 2005). Columns (Strata X, Phenomenx, 8BS100TAK) were conditioned with 1.0 ml 100% methanol and 1.0 ml distilled water. After adding the sample at 1.0 ml, the sample was washed with 5% methanol. Steroids were eluted off the column with 2.0 ml of 100% methanol, then evaporated and reconstituted in 1.0 ml 30% methanol. Samples were then refrigerated until assayed.

Fecal Cortisol Validation

A pilot study conducted in RNP in May-July 2000 determined that fecal samples could be collected from *Eulemur rubriventer* according to the methods below (Tecot, 2001)**.** Validation procedures were carried out with the help of D. Wittwer at the WNPRC Assay Services Laboratory. Cortisol values were determined by enzyme immunoassay (EIA; see below). Validations consisted of tests of accuracy and parallelism (see Whitten *et al.,* 1998a). Parallelism was achieved by adding 300 µl of fecal extract to 7.2 µl of the standard and serially diluting with ethanol (1:1) 8 times. 100 µl of each dilution was evaporated and assayed by EIA. Parallelism was assessed by comparing the slope of the curve with that of the standard curve. Accuracy was achieved by adding 100 µl *Eulemur* fecal sample pool in duplicate to each of the standard curve points and means are given with standard error (SEM).

Validations established that the cortisol EIA resulted in reliable measures of cortisol concentrations in *E. rubriventer* fecal extracts. The slope of the serially diluted

fecal extracts was not significantly different than the slope of the standard curve ($t_{[22]}$=1.85, ns, p>.05) and parallelism was achieved. Accuracy for added *E. rubriventer* feces to the standard curve points was determined to 96.68 ± 1.79% SEM, n=6.

Enzyme Immunoassays

Following the protocol used by Ziegler and colleagues (1995), with the modification of standards prepared in alcohol (reported in Sousa and Ziegler, 1998), samples from adults were assayed in duplicate and hormone concentrations are expressed in ng/g feces (n=922). 100 µl of each sample were evaporated and then diluted 1:2 in EIA buffer prior to enzyme immunoassay. 250 µl enzyme-labeled antigen (horseradish peroxidase cortisol) was added to the standards and each sample, and 100 µl of the mixture was added to each well in the plate for binding during a 2-hour incubation. Solid-phase washing separated bound and free cortisol. 100 µl substrate were then added, and absorbance was calculated.

Coefficients of variation (CV) were calculated for intra- and inter-assay variation of the fecal pool. Inter-assay CVs for cortisol were 16.0% for the low pool (n=30) and 11.9% for the high pool (n=31). Intra-assay CVs for cortisol were 3.6% for the low pool (n=30) and 2.1% for the high pool (n=31).

Climate

To test the predictions related to climate seasonality, temperature and precipitation were used as indices of climatic change. In each site minimum and maximum temperatures were recorded in degrees Celsius each day and rain was collected in a rain gauge and measured in millimeters each morning, or in the case of high rain

volume, when full throughout the day. Monthly temperature means were used to determine cool and warm seasons and monthly precipitation totals were used to determine dry and wet seasons (Figure 4.2). No differences between sites were found and data were pooled. Annual precipitation between January 2004 and December 2004 totaled 4060 mm (range 73.56 mm - 701 mm). For details, see Tecot, Chapter 2.

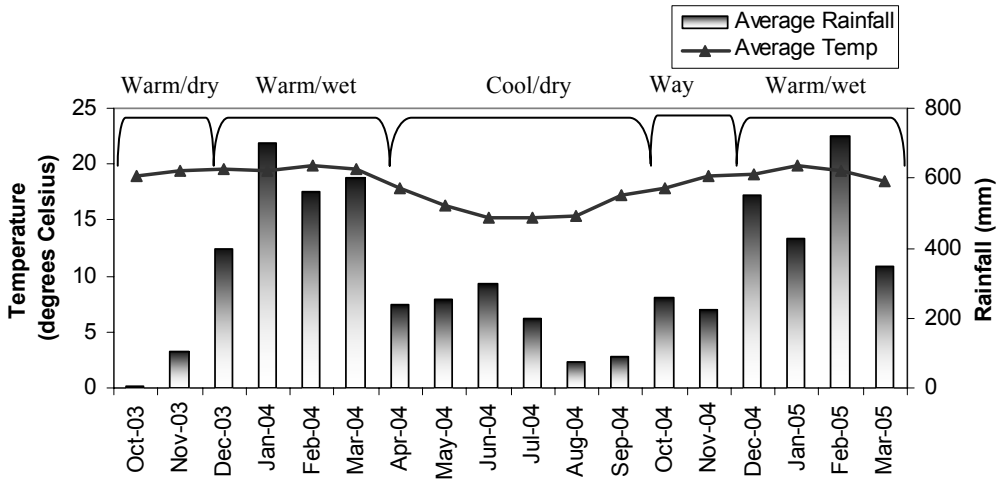


Figure 4.2. Monthly mean precipitation (mm) and total temperature (˚C).

Phenology

To test the predictions related to food availability and site differences, phenological assessments were made at each site according to the methods in Overdorff (1991, 1996a). Three botanical plots (100 x 10, 5 x 50, 10 x 25) were established at each site within known *Eulemur rubriventer* home ranges (highland, slope, valley). Initially, all trees and lianas 2.5 cm diameter at breast height (DBH) or larger (n=1674) were marked and identified by common Malagasy name with the help of local research technicians. Later species designations were determined using published work by Overdorff (1991), Turk (1995), and the Missouri Botanical Garden database. The

availability of fruits (ripe, unripe), flowers (buds, blooms), and leaves (immature, mature) was recorded for each marked tree on a scale of 0 (absent) to 5 (full abundance) every month (Oates, 1977; Overdorff, 1996a).

Food availability seasons were determined by totaling the number of trees and lianas with a score of 1-5 for each food item in each phenophase, and dividing by the total number of trees and lianas assessed each month in each site. Food abundance and scarcity seasons did not completely coincide with previous studies (see Overdorff and Tecot, 2006; Tecot, Chapter 2), and differences between sites were apparent. Mature leaves were abundant throughout the year with no fluctuation in availability, so although they were a food source they were not used to show fluctuations in food availability. As ripe fruit seasons influenced behavior, seasons were divided into ripe fruit abundance and ripe fruit scarcity (Figure 4.3) (see Tecot, Chapter 3 for details).

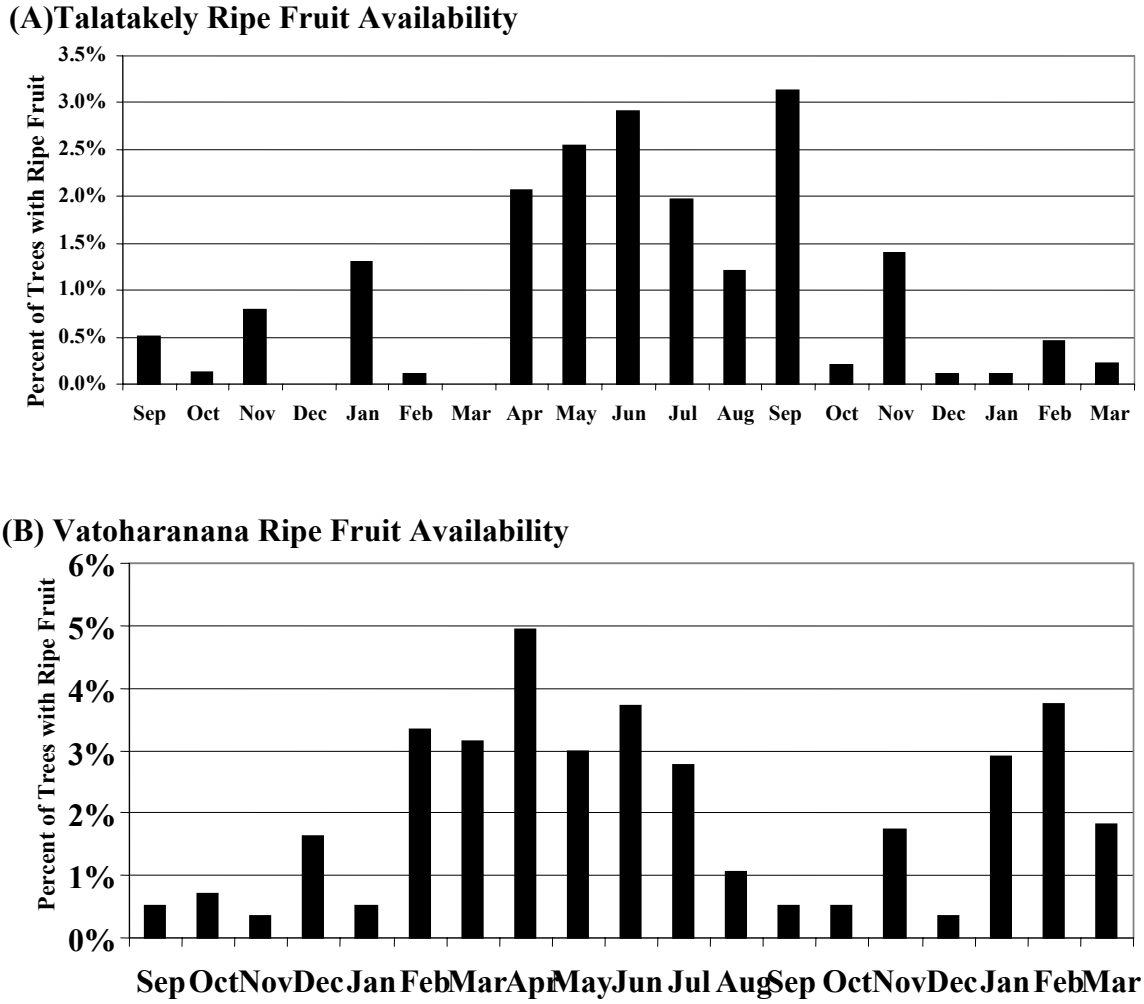


Figure 4.3. Fruit availability in each site. Proportion of trees in (A) Talatakely and (B) Vatoharanana botanical plots with scores of 1-5 for ripe fruit each month.

Behavior

To estimate an overall time budget for the red-bellied lemur, 17 behaviors in 6 categories were recorded (see Chapter 3). All occurrences of aggressive, feeding,

grooming, resting, traveling, and playing behaviors were recorded for eight hours per day (within 0700-1600), 5 days per week, rotating focal animals daily. Time budgets were calculated based upon 2586 hours of continuous focal animal sampling (Altmann, 1974), and were compiled for each adult and juvenile individual (n=17) (Table 4.3). A category termed 'total activity' was later calculated as the combined proportion of time spent traveling and feeding. Weekly mean proportions of time each individual devoted to each behavioral category from January 2004 – March 2005 were combined to construct time budgets for each site (n=2), group (n=5), and the species in general. See Tecot, Chapter 3 for details.

Data Analysis

Because lowest fecal cortisol levels approached zero, analyzing by percent increase from baseline would not provide different results, so all cortisol levels are expressed in ng/g feces. Fecal cortisol levels were not normally distributed and were log-transformed to meet the criteria of parametric tests. Data were standardized to z-scores to observe correlations between cortisol and behavior. Reproductive stages are noted for reference, but not analyzed in this study. All analyses were performed using the SPSS Program for Windows, version 15.0 (SAS Institute, Cary, NC). A Linear Mixed-Effects Model (multi-level modeling) procedure (MIXED) was employed because it has the advantage of analyzing unbalanced data sets and has been found appropriate for analyses of cortisol (Hruschka *et al.,* 2005), which are complicated by inter- and intra-individual variation. This method is ideal when analyzing repeated measures and longitudinal data, and further enables habitat and seasonal comparisons of cortisol levels. It is also a more conservative estimate of significance compared with General Linear Models when

correlations are suspected in the data. The REPEATED subcommand was used to model the possible correlation of the residual errors with each individual. MIXED was used to construct a least squares model to test all relationships with fecal cortisol levels, including whether there was an effect of sex (n_{female} = 413, n_{male} = 507; 3 remaining samples from unidentified individuals not included in this analysis). Significance was set at $p<.05$. Significance is denoted using standard notation: * $P<.05$; ** $P<.01$; *** $P<.001$ (Sokal and Rohlf, 1981).

RESULTS

Overall and Monthly Cortisol Levels

Species-Wide Cortisol: 922 fecal samples collected over the course of nineteen months from 11 adult individuals (comprising 664 individual-weeks) in both sites were assayed. No significant differences in fecal cortisol (fC) levels were observed between the sexes, $F(1,260.448)=0.590$, $p=0.443$, so data were combined. Individual fC levels from the entire study ranged from 0.85ng/g to 323.10ng/g (n=922), a rise above baseline levels of over 300%, and the mean for all samples was 28.78 $\pm$ 26.38 (SD) (Table 4.4).

To estimate the effects of month on fecal cortisol levels, data were analyzed using a Mixed Model with month as a fixed effect, and fC levels were predicted based upon week with individual ID repeated. Monthly differences were apparent, $F(16,318.710)=4.528$, $p<.001$ (Figure 4.4), with significant differences occurring between several months (Table 4.5). The months preceding and following gestation were exceptional: in March through May 2004 cortisol levels were significantly lower than most months, and in September through November 2004 cortisol levels were significantly

higher than most other months (Figure 4.4, Table 4.5). The only inter-annually significantly different month was November.

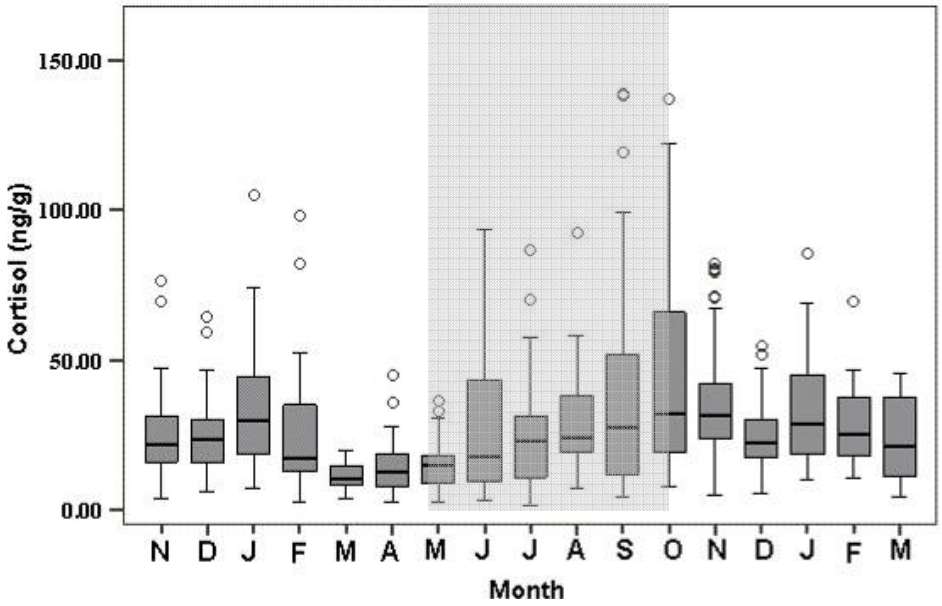


Figure 4.4. Boxplot of monthly cortisol levels in all individuals from November, 2003 through March, 2005. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and open circles indicate outliers. The shaded area indicates the period of gestation (Tecot, this study).

Table 4.4. Descriptive statistics for individuals' fecal cortisol excretion by (A) sample, (B) weekly mean, and (C) monthly mean, overall and by site.

(A) Individual Samples

	Minimum	Maximum	Variance	Standard Deviation	Mean	N
Talatakely	1.5	137	358.96	18.95	24.71	465
Vatoharanana	0.85	323.10	1005.84	31.71	32.92	457
Total	0.85	323.10	695.73	26.38	28.78	922

(B) Weekly Samples by Individual

	Minimum	Maximum	Variance	Standard Deviation	Mean	N
Talatakely	3.05	137.00	301.19	17.35	24.33	346
Vatoharanana	1.32	161.98	722.81	26.89	32.10	318
Total	1.32	161.98	517.40	22.75	28.05	664

(C) Monthly Samples by Individual

	Minimum	Maximum	Variance	Standard Deviation	Mean	N
Talatakely	5.63	69.59	143.16	11.96	24.56	110
Vatoharanana	6.88	93.25	347.92	18.65	32.82	85
Total	5.63	93.25	247.96	15.75	28.16	195

Table 4.5. Matrix of significance values for monthly pairwise comparisons of fecal cortisol levels from November, 2003 though March, 2005. Bolded p-values are significant.

	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
D	.848															
J	.070	**.037**														
F	.893	.756	.103													
M	**.019**	**.026**	**.000**	**.014**												
A	**.029**	**.039**	**.000**	**.026**	.666											
M	.068	.090	**.001**	.061	.575	.842										
J	.704	.580	.201	.808	**.012**	**.018**	**.039**									
J	.641	.516	.210	.749	**.008**	**.012**	**.030**	.945								
A	.896	.757	.108	.997	**.017**	**.026**	.060	.805	.735							
S	**.010**	**.005**	.505	**.021**	**.000**	**.000**	**.000**	.051	.051	**.015**						
O	**.001**	**.000**	.158	**.003**	**.000**	**.000**	**.000**	**.009**	**.009**	**.003**	.402					
N	**.011**	**.005**	.471	**.021**	**.000**	**.000**	**.000**	**.050**	**.050**	**.020**	.933	.466				
D	.969	.896	.084	.871	**.029**	**.046**	.093	.693	.635	.873	**.015**	**.002**	**.012**			
J	.157	.108	.800	.215	**.001**	**.001**	**.003**	.337	.355	.212	.380	.117	.354	.155		
F	.635	.506	.189	.748	**.006**	**.009**	**.026**	.953	.992	.744	**.041**	**.006**	**.041**	.629	.310	
M	.770	.893	.055	.687	.059	.095	.165	.536	.482	.688	**.009**	**.001**	**.009**	.810	.115	.451

Cortisol x Site: Visual inspection indicates that patterns were similar in general, but slightly unsynchronized with a few divergences (Figure 4.5). The magnitude of all fluctuations was greater in Vatoharanana, the undisturbed site, as indicated by the larger variance in each subject's individual, weekly, and monthly mean fecal cortisol measures (Table 4.4). Baseline levels were lowest in the undisturbed site (Table 4.4) and lowest levels occurred March–May. Durations of peaks were similar, with the exception of September–November, 2004 when cortisol level elevations in the undisturbed population were sustained (Figure 4.5).

In a Mixed Model estimating fC levels by site, based upon month with group repeated, sites were significantly different, $F(1,14.384)=12.726$, $p<.01$, although the ranges of cortisol levels expressed in each site were similar (Table 4.6). Contrary to

predictions, undisturbed forest groups had higher fC levels (N=664 individual-weeks, 924 samples) (Figure 4.6).

To determine the timing of significant differences between sites, the same model was run with month as a covariate and a site by month interaction, and fC levels differed significantly across sites, $F(1,84.234)=7.733$, $p<.01$, as predicted. Contrary to predictions, fC levels varied significantly across months only in Vatoharanana, $F(16,109.752)=6.179$, $p<.001$, and not in Talatakely, $F(16,120.311)=0.913$, $p=.556$. However, fC levels in Talatakely in March were significantly lower than several other months: fC levels in March 2004 were significantly lower than all other months except November 2003 and March 2005; fC levels in March 2005 were significantly lower than all other months except November 2003, March –May 2004 and September 2004.

An interaction between site and month indicated significantly different fC levels in five months between sites, $F(16,115.486)=3.053$, $p<.001$, during which fC levels in Vatoharanana, the undisturbed site, were higher than those in Talatakely, the disturbed site (Figure 4.7; Table 4.7). The model reported here was chosen based upon comparison of fit using Akaike's Information Criterion (AIC, Akaike, 1973). However, as only slight differences between the fit of different models existed, it should be noted that fC levels in April, November, and March were significantly different among sites in more than one model (*e.g.,* using a first-order autoregressive covariance matrix rather than a diagonal matrix).

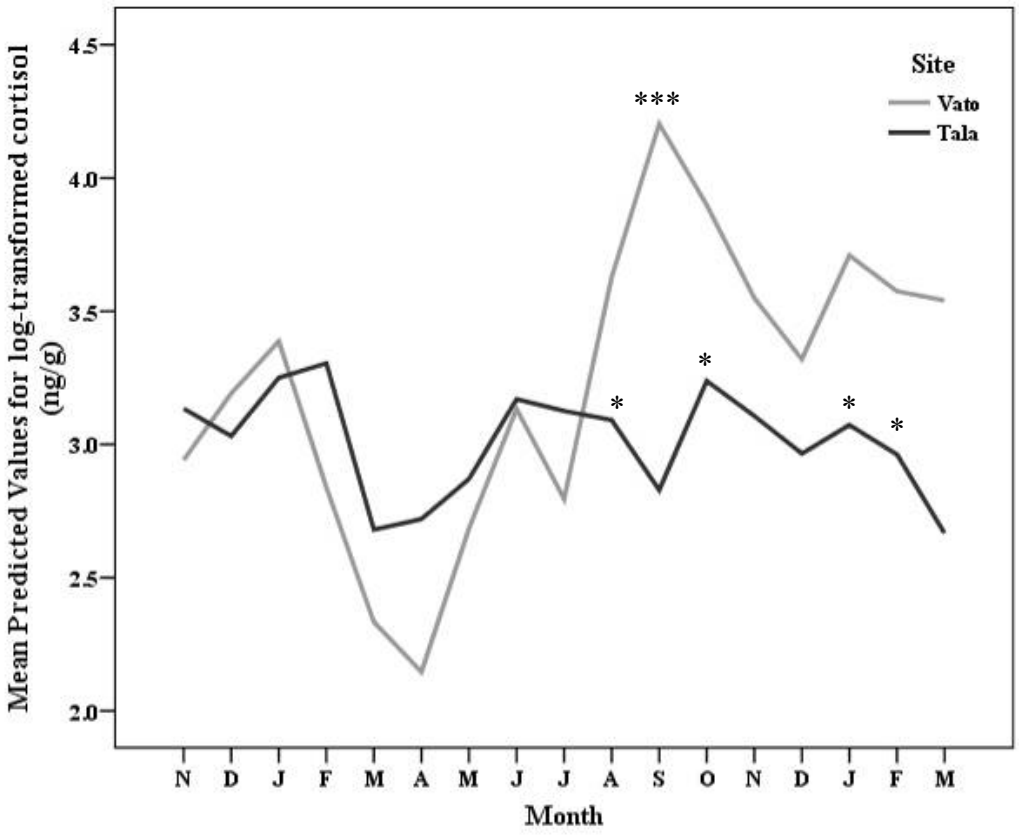


Figure 4.5. Monthly mean predicted values for log-transformed fecal cortisol levels (ng/g) at each site throughout the study. Cortisol levels differed significantly between sites in 5 months: August, September, October, January, and February.

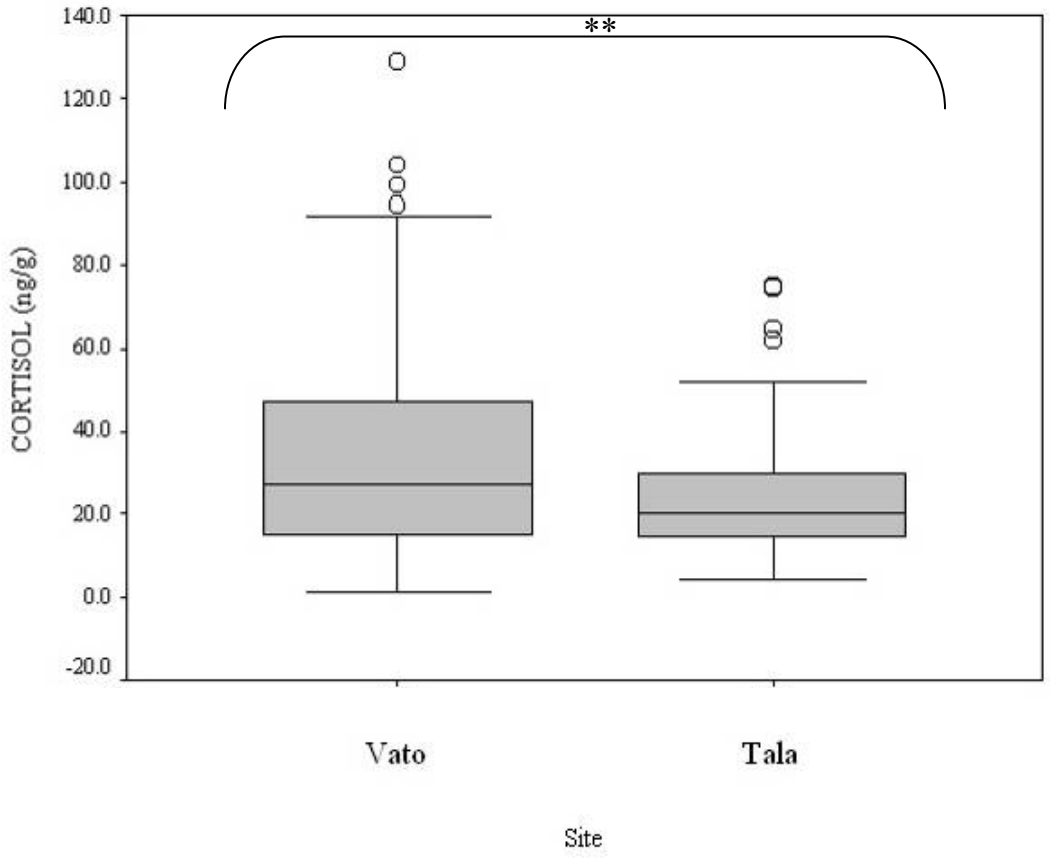


Figure 4.6. Boxplot of total mean fecal cortisol levels (ng/g) in each site for all months. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and circles indicate outliers.

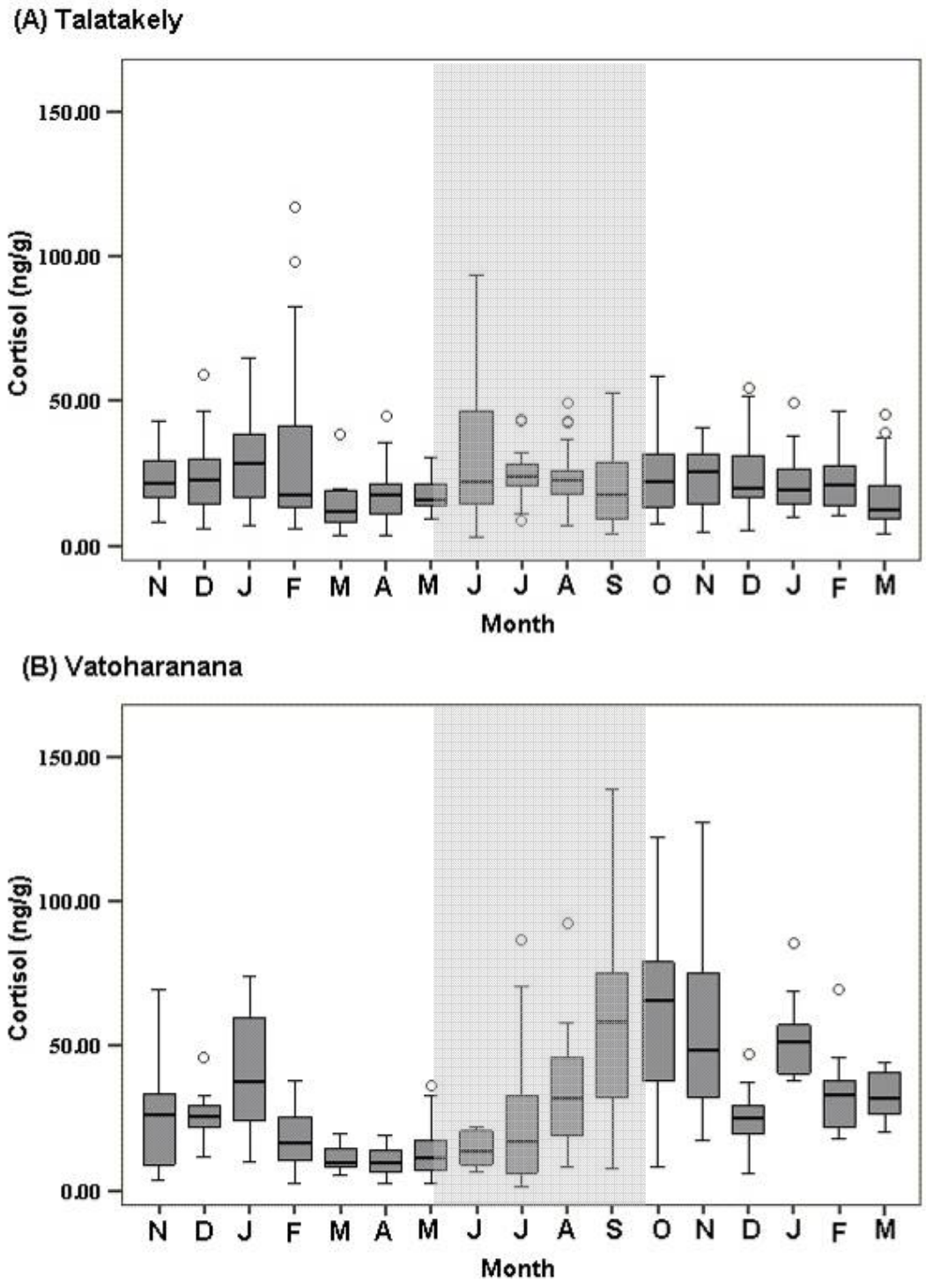


Figure 4.7. Boxplot of mean monthly fecal cortisol levels (ng/g) in (A) Talatakely and (B) Vatoharanana. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and open circles indicate outliers. Gestation is highlighted in gray.

Seasonal Cortisol Levels

Fecal cortisol levels were estimated in Mixed Models with site, season (temperature or rainfall, individually, and ripe fruit), and site by season interactions (site x rainfall, site x temperature, site x ripe fruit), based upon month with individual ID repeated. Separate models were used since a three-way interaction between seasons could not be determined to create estimated marginal means.

Climate Seasons

Cortisol x Temperature: Though fC levels were higher during the cool season, no significant differences in fC levels were found among temperature seasons, $F(1,20.311)=3.797$, $p=.065$, indicating no significant effect of temperature upon fC levels (Figure 4.8).

Cortisol x Temperature x Site: Site by season interactions indicated that site had no effect upon the relationship between temperature and fC levels, $F(1,20.311)=1.890$, $p=.184$.

Cortisol x Rainfall: There was a significant effect of rainfall on fC levels with elevations occurring during the dry season, $F(1,21.963)=18.215$, $p<.001$ (Figure 4.9).

Cortisol x Rainfall x Site: The relationship between fC levels and precipitation was variable among sites, $F(1,21.963)=9.825$, $p=.005$. Both sites excreted higher fC levels during the dry season, but this relationship was only significant in Vatoharanana, $F(1,21.963)=22.832$, $p<.001$, and not in Talatakely, $F(1,21.963)=0.803$, $p=.380$ (Figure 4.10), contrary to expectations. FC levels were significantly higher in Vatoharanana than in Talatakely during both precipitation seasons, though this relationship was stronger

during the dry season, F(1,13.396)=28.422, p<.001, than the wet season, F(1,9.542)=5.308, p=.045 (Figure 4.10). Though a stronger relationship was predicted during the wet season, these data support the prediction that stronger relationships would be apparent during the most challenging seasons. Figure 4.11 further demonstrates how the strength of this relationship diverged across sites.

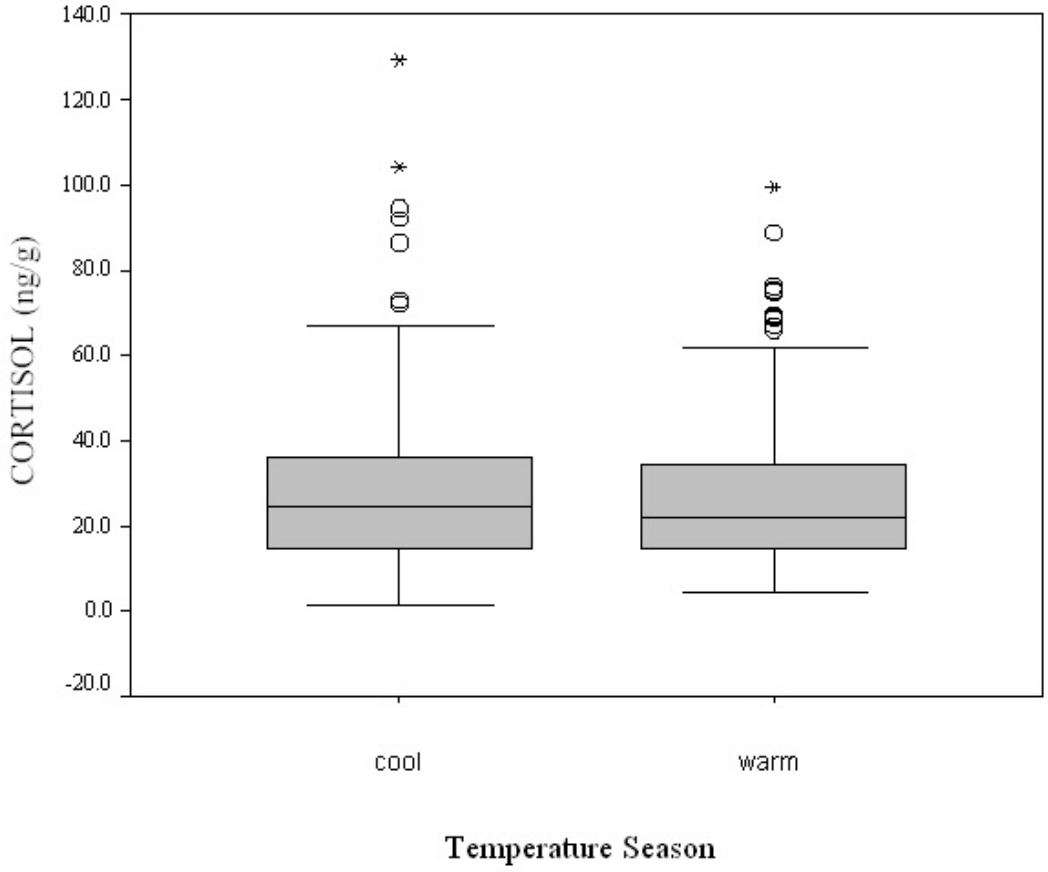


Figure 4.8. Boxplot of site differences in fecal cortisol levels (ng/g) during temperature (cool and warm) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and circles indicate outliers. Stars indicate extreme cases.

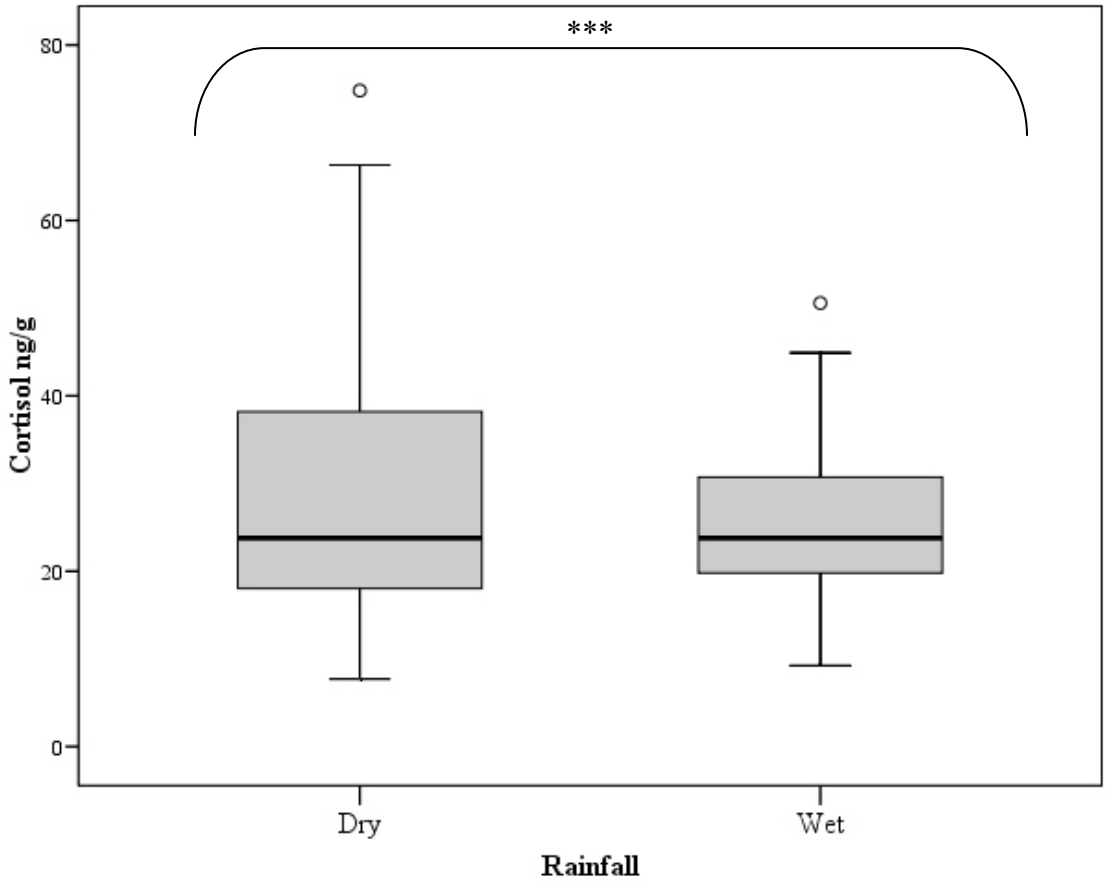


Figure 4.9. Boxplot of monthly fecal cortisol levels (ng/g) in dry and wet seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and open circles indicate outliers.

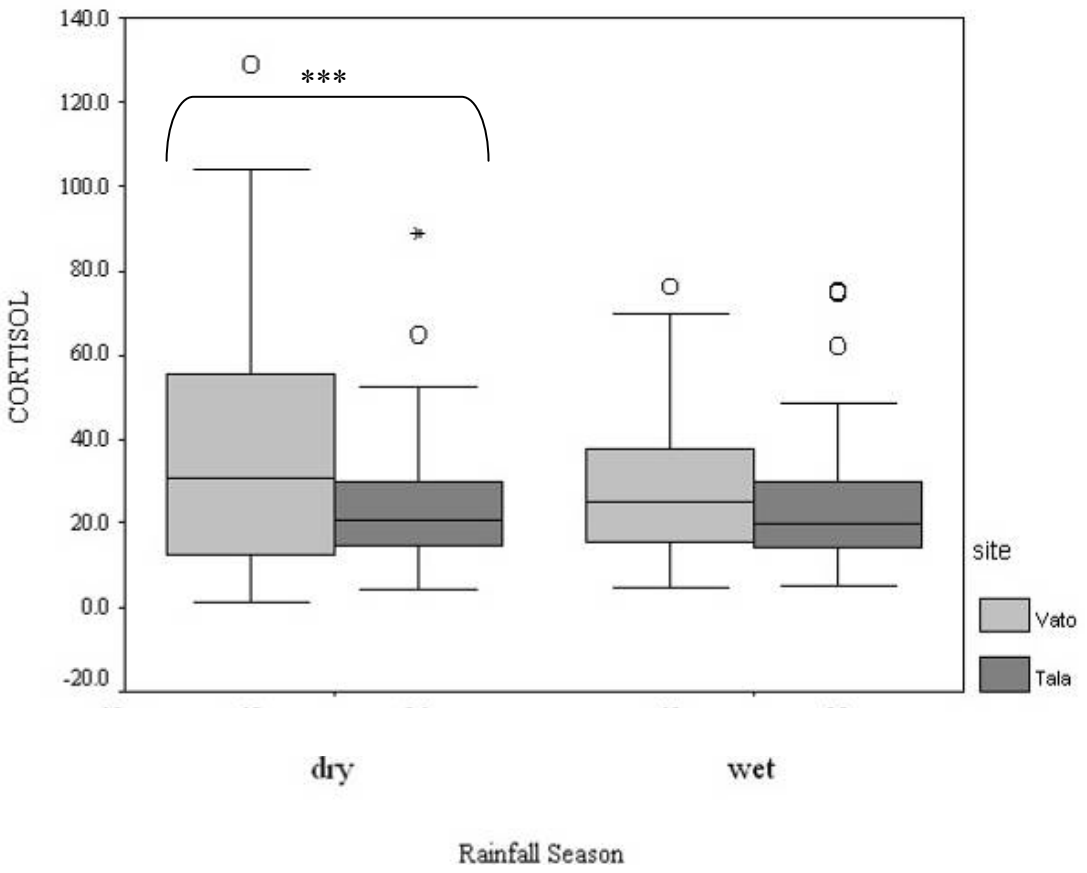


Figure 4.10. Boxplot of site differences in fecal cortisol levels (ng/g) during precipitation (dry and wet) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and circles indicate outliers. Stars indicate extreme cases.

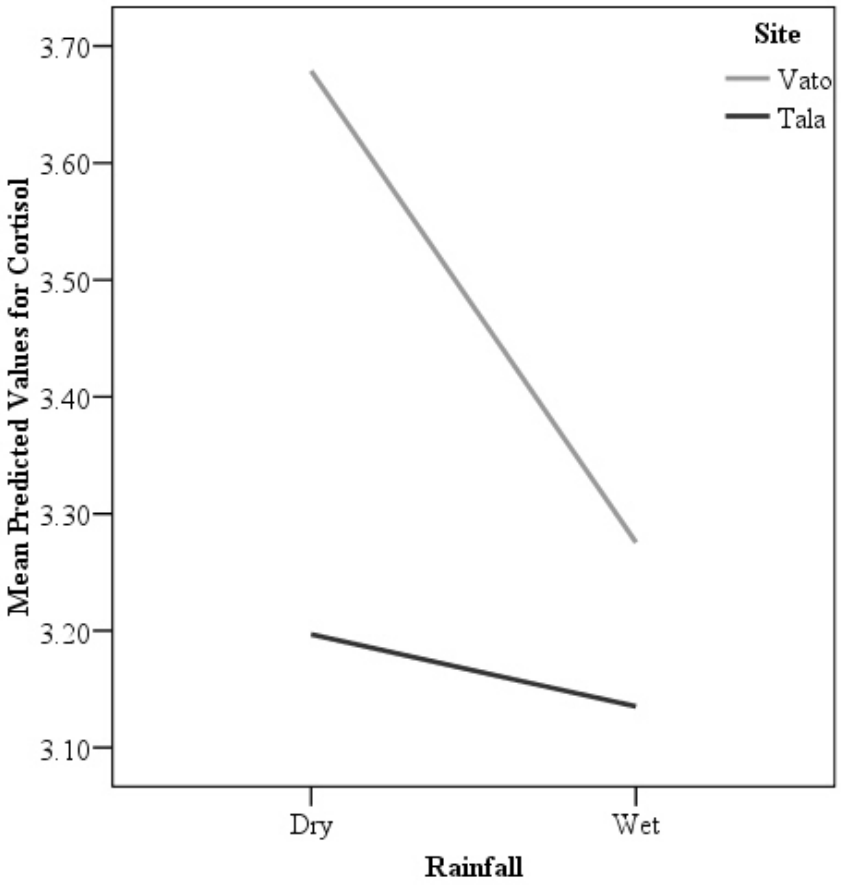


Figure 4.11. Mean predicted values for cortisol (ng/g) in dry and wet seasons by site.

Ripe Fruit Availability Seasons

Cortisol x Fruit: Differences in fC levels were found among ripe fruit availability seasons, where fC levels were significantly higher during the scarce season, $F(1,275.459)=32.122$, $p<.001$ (Figure 4.12).

Cortisol x Fruit x Site: A significant interaction between ripe fruit availability season and site fC levels, $F(1,275.459)=26.020$, $p<.001$, indicated that sites showed different patterns. While fC levels were higher during ripe fruit scarcity overall, this effect was only significant in Vatoharanana, the undisturbed site, $F(1,219.221)=52.632$,

p<.001 (Figure 4.13a). Differences across fruit availability seasons were not significant in Talatakely, the disturbed site, F(1,367.711)=0.179, p=.673 (Figure 4.13b), indicating a weaker response to fluctuations in fruit availability in that site.

Within each fruit availability season interesting site differences emerged. FC levels were higher in the Talatakely, the disturbed site, than in Vatoharanana during the abundant season as predicted F(1,220.547)=5.009, p=.026. Contrary to expectations though, fC levels were significantly higher in Vatoharanana than in Talatakely during the scarce season, F(1,202.501)=24.124, p<.001 (Figure 4.14). Higher fC levels in Talatakely compared with Vatoharanana during fruit abundance may be a relic of their largely invariable profile, while fC levels in Vatoharanana fluctuate about their mean, with similar baseline levels among sites.

Cortisol x Fruit x Site x Rainfall: To determine if the relationship between fC levels and rainfall was partially due to the relationship between rainfall and fruiting, fC levels were estimated in a Mixed Model with ripe fruit season, rainfall season, site, and their interactions. Rainfall was no longer significant, F(84.404)=0.665, p=.407. Significant 3-way interactions, F(1,107.920)=5.845, p<.001, indicated that differences between rainfall seasons only occurred during fruit scarcity in Vatoharanana; differences between fruit seasons only occurred during the dry season in Vatoharanana; and site differences only occurred during the dry scarce season (Table 4.8).

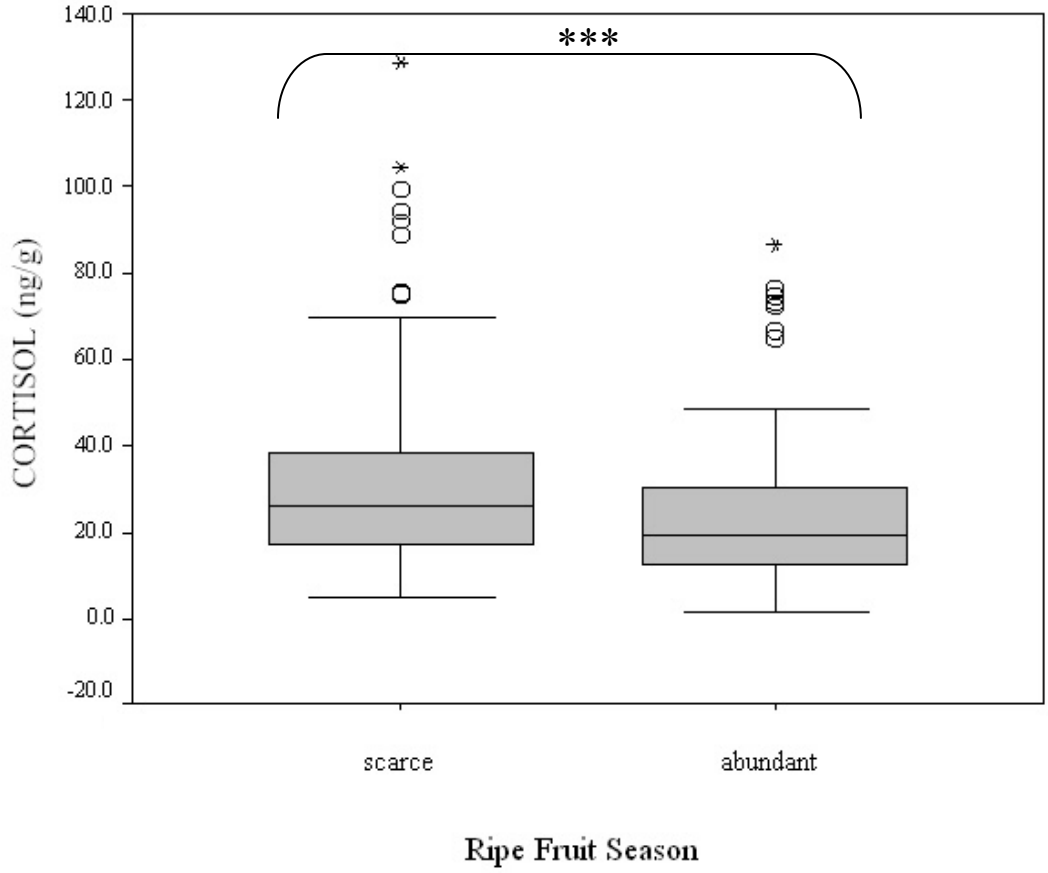


Figure 4.12. Boxplot of mean fecal cortisol levels (ng/g) in each ripe fruit season. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and open circles indicate outliers. Stars indicate extreme cases.

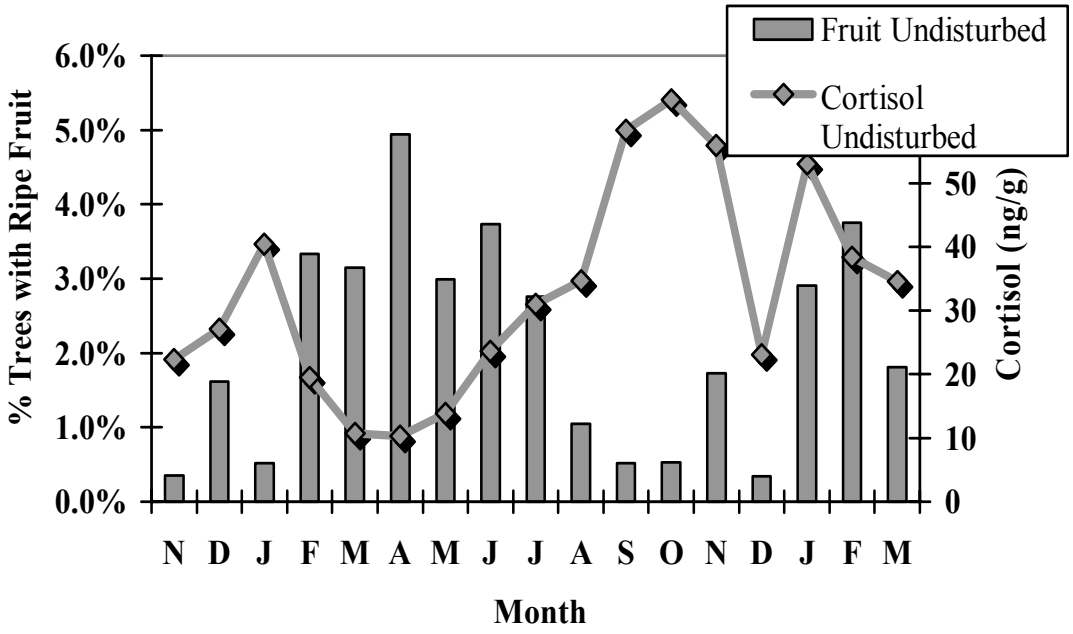
Table 4.6. Summary statistics for weekly mean fecal cortisol levels in Talatakely and Vatoharanana from November, 2003 through March, 2005.

Site	**Mean**	**N**	**Std. Deviation**	**Range**
Talatakely	24.33	346	17.35	133.95
Vatoharanana	32.10	318	26.89	160.66

Table 4.7. Pairwise comparisons of estimated marginal means of log-transformed fecal cortisol levels among sites. Months in which sites differed significantly are bolded.

November	1	102.439	.461	.499
December	1	98.013	.373	.543
January	1	108.503	.231	.632
February	1	111.839	2.403	.124
March	1	106.742	1.392	.241
April	1	109.882	3.824	.053
May	1	127.236	.323	.571
June	1	97.559	.017	.897
July	1	118.806	1.070	.303
August*	**1**	**96.382**	**4.274**	**.041**
September***	**1**	**104.239**	**22.579**	**.000**
October*	**1**	**99.540**	**5.700**	**.019**
November	1	93.435	2.819	.096
December	1	184.847	.737	.392
January*	**1**	**95.663**	**5.508**	**.021**
February*	**1**	**99.017**	**4.623**	**.034**
March	1	247.483	3.238	.073

(A)



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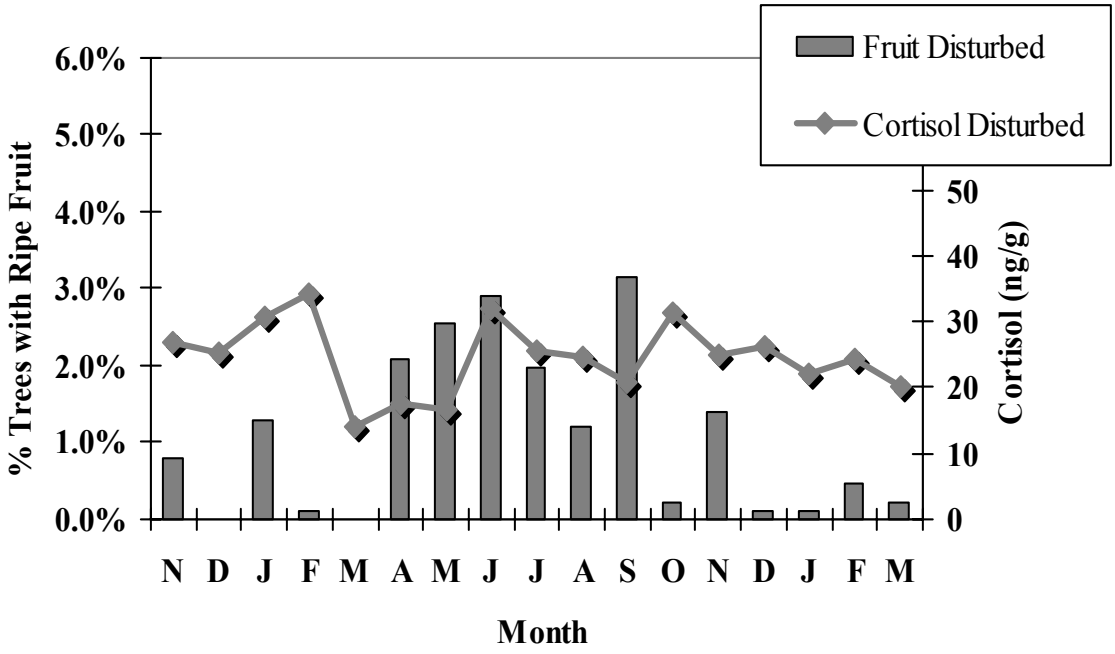


Figure 4.13. Ripe fruit availability and fecal cortisol levels (ng/g) in (A) Vatoharanana and (B) Talatakely.

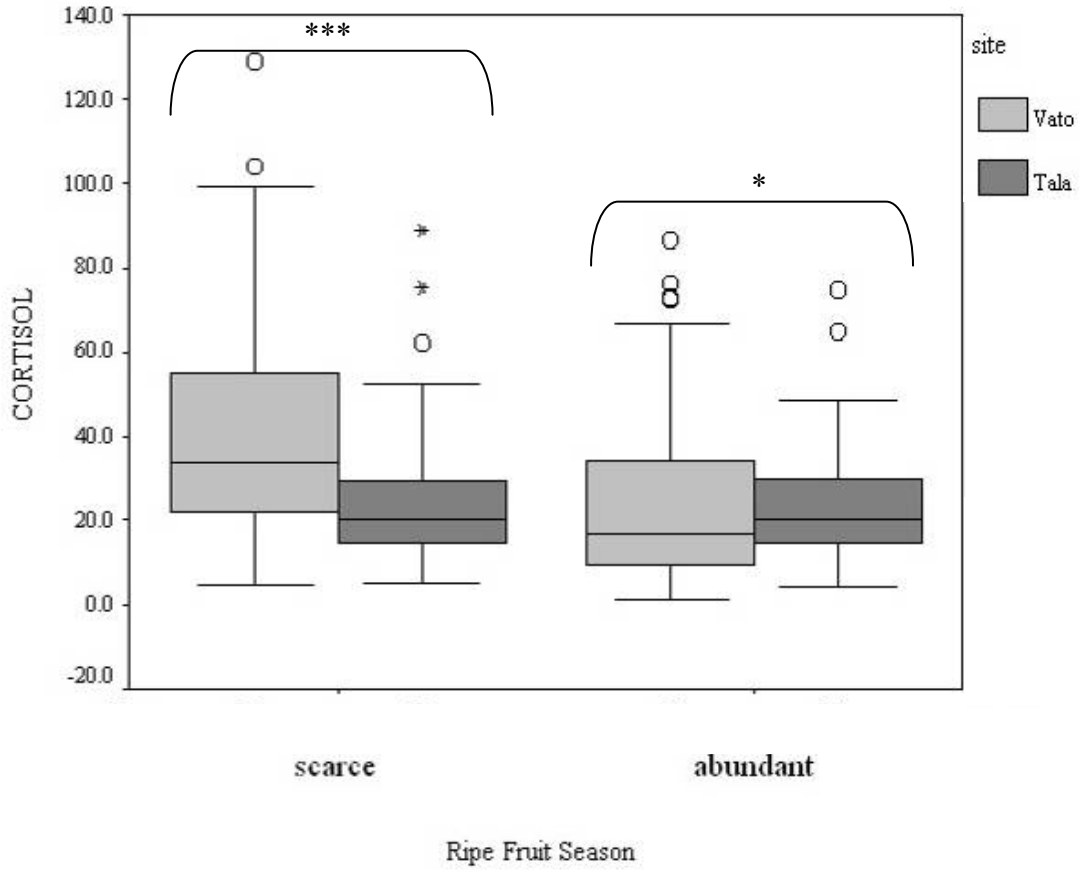


Figure 4.14. Boxplot of site differences in fecal cortisol levels (ng/g) during ripe fruit (scarce and abundant) seasons. The line within the box is the median based on weekly means, the box encloses 25%-75% of the data, the whiskers outside the box enclose 5%-95% of the data, and circles indicate outliers. Stars indicate extreme cases.

Table 4.8. Pairwise comparisons for three-way interactions among precipitation seasons, ripe fruit availability seasons, and log-transformed values of cortisol (ng/g). Significant values are bolded.

Ripe Fruit Season	Site	Rainfall Season (A)	Rainfall Season (B)	Mean Difference (A-B)	Standard Error	df	Sig.
Scarce	**Vato (undisturbed)**	**Dry**	**Wet**	**.558****	**.178**	**93.655**	**.002****
		Wet	**Dry**	**-.558****	**.178**	**93.655**	**.002****
	Tala (disturbed)	Dry	Wet	.204	.163	124.758	.213
		Wet	Dry	-.204	.163	124.758	.213
Abundant	Vato (undisturbed)	Dry	Wet	-.332	.183	91.910	.073
		Wet	Dry	.332	.183	91.910	.073
	Tala (disturbed)	Dry	Wet	-.146	.157	96.080	.355
		Wet	Dry	.146	.157	96.080	.355

Precipitation Season	Site	Ripe Fruit Season (A)	Ripe Fruit Season (B)	Mean Difference (A-B)	Standard Error	df	Sig.
Dry	**Vato (undisturbed)**	**Scarce**	**Abundant**	**1.013*****	**.182**	**84.327**	**.000*****
		Scarce	**Abundant**	**-1.013*****	**.182**	**84.327**	**.000*****
	Tala (disturbed)	Scarce	Abundant	.240	.152	202.134	.117
		Scarce	Abundant	-.240	.152	202.134	.117
Wet	Vato (undisturbed)	Scarce	Abundant	.123	.176	120.708	.488
		Scarce	Abundant	-.123	.176	120.708	.488
	Tala (disturbed)	Scarce	Abundant	-.109	.160	94.665	.494
		Scarce	Abundant	.109	.160	94.665	.494

Precipitation Season	Ripe Fruit Season	Site (A)	Site (B)	Mean Difference (A-B)	Standard Error	df	Sig.
Dry	**Scarce**	**Vato (undisturbed)**	**Tala**	**.564****	**.182**	**98.164**	**.002****
		Tala (disturbed)	**Tala**	**-.564****	**.182**	**98.164**	**.002****
	Abundant	Vato (undisturbed)	Tala	-.209	.163	87.512	.204
		Tala (disturbed)	Tala	.209	.163	87.512	.204
Wet	Scarce	Vato (undisturbed)	Tala	.210	.162	95.351	.198
		Tala (disturbed)	Tala	-.210	.162	95.351	.198
	Abundant	Vato (undisturbed)	Tala	-.022	.180	88.557	.902
		Tala (disturbed)	Tala	.022	.180	88.557	.902

Behavioral and Physiological Mechanisms

Analyses of cortisol and behavior were conducted on data collected January, 2004 though March, 2005, as behavioral data did not begin until January, 2004. Correlations were run with log-transformed weekly mean individual cortisol values to view the relationship between cortisol and behavior (total activity, feeding, resting, traveling), overall and among sites.

To further estimate the relationship between cortisol and behavior, cortisol values and the time spent feeding, resting, and traveling were standardized into z-scores, and log-transformed fC levels were estimated in Mixed Models with site, percent time feeding, resting, and traveling, and the interaction between site and each behavior. Cortisol was based on week with individual ID repeated.

To determine whether the relationship between cortisol and behavior varied by season, the same Mixed Models were run with one of three seasons (temperature, rainfall, ripe fruit availability) and their interactions with each behavior (feeding, resting, traveling), based on month with individual ID repeated. Site and three-way interactions between site, behavior, and season were included in the model to further assess the influence of habitat quality on these relationships. Separate models were used for each season since a three-way interaction between seasons could not be determined to create estimated marginal means.

Because the proportion of time resting was highly negatively correlated with feeding, r=.-.769, p<.001, n=273, and traveling, r=-.758, p<.001, n=273, standardized z-scores for feeding and traveling were entered into the model independently from resting to best assess the unique effects of these predictors upon cortisol levels. It is thus unknown whether the observed results for the relationship between cortisol levels and

percent time traveling and feeding are indeed due strictly to traveling and feeding, and not partially due to resting.

Overall and Monthly Cortisol Levels and Behavior

Cortisol x Behavior: In a two-tailed Pearson correlation, log-transformed weekly mean individual cortisol levels were significantly positively correlated with total proportion of time active (feeding and traveling combined), r=.163, p=.011, n=240, feeding, r=.145, p=.024, n=240, and traveling r=.130, p=.045, n=240. Cortisol levels and the proportion of time resting were inversely related, r=-.123, p=.058, n=240, though this relationship was not significant. Contrary to expectations, Mixed Model analyses indicated that none of these behaviors were *significant predictors* of cortisol levels (Table 4.9).

Cortisol x Behavior x Site: In a two-tailed Partial Correlation between weekly mean individual log-transformed fC levels and behavior controlling for site, significant positive correlations remained between activity level and fC levels, r=.143, p=.027, n=237, and traveling and fC levels, r=.132, p=.042, n=237, as did the non-significant negative relationship between resting and fC levels, r=-.101, p=.119, n=237. These results indicate that the relationships between fC levels and total activity level, traveling, and resting were consistent across sites. However, there was an effect of site on the association between fC levels and feeding, and the significant positive relationship was eliminated, r=.113, p=.082, n=237.

Although correlations and visual inspection indicated stronger relationships between behavior and cortisol in Vatoharanana, the undisturbed site (Figure 4.15), Mixed Models determined that the relationship between cortisol and each behavior (feeding,

resting, and traveling) did not significantly differ by site (Table 4.10), indicating that behavior was not more predictive of fC levels in either site.

The timing of changes in the relationships between resting, feeding, and cortisol throughout the study elucidates periods of energy expenditure, storage, conservation, and maximization (Figure 4.16). Table 4.11 summarizes these periods in each site.

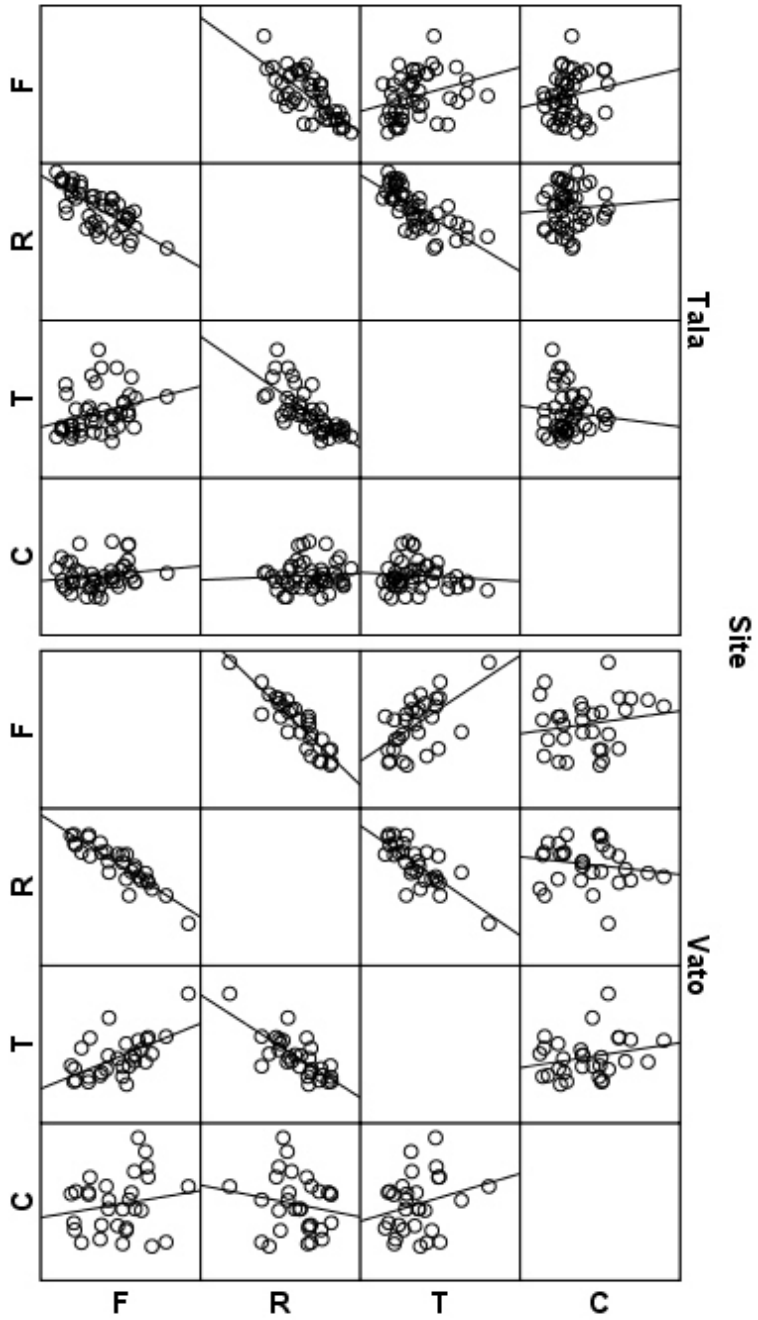


Figure 4.15. Scatter plot matrix of the relationship between behaviors and cortisol in both sites based on monthly means. Feeding (F), resting (R), and traveling (T) have stronger relationships with cortisol (C) in Vatoharanana, the disturbed site.

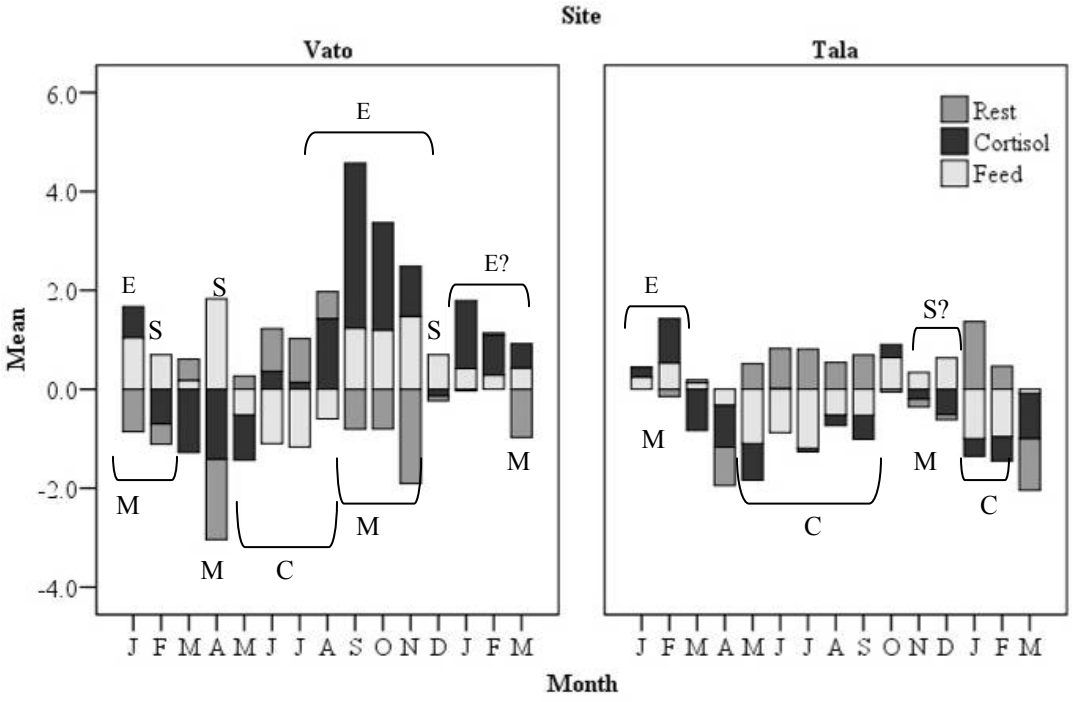


Figure 4.16. Monthly relationship between fecal cortisol, resting, and feeding in both sites from January, 2004 through March, 2005. 'E' denotes periods of energy extraction where the proportion of time resting is minimal, cortisol levels are high, and the proportion of time feeding may be variable; 'S' denotes periods of energy storage where resting and cortisol levels are low and the proportion of time spent feeding is high. 'C' denotes periods of energy conservation where the proportion of time resting is high and feeding and cortisol levels are minimal; 'M' denotes periods of energy maximization where the proportion of time resting is minimal, feeding is high, and cortisol levels may be variable.

Table 4.9. Parameter estimates of covariance between standardized values of logged cortisol (ng/g) and behavior. Significant results are bolded.

Standardized Predictor	**Estimate**	**Standard Error**	**df**	**t-value**	**Significance**
Feeding	.087	.069	235.759	1.259	.209
Resting	-.092	.063	225.229	-1.473	.142
Traveling	.099	.061	215.016	1.608	.109
Feeding*Temperature	**-.353**	**.162**	**234.093**	**-2.181**	**.030***
Resting*Temperature	**.334**	**.136**	**217.008**	**2.445**	**.015***
Traveling*Temperature	-.238	.131	212.399	-1.822	.070
Feeding*Rainfall	-.145	.133	234.726	-1.088	.278
Resting*Rainfall	.155	.128	215.246	1.152	.250
Traveling*Rainfall	-.176	.134	190.984	-1.320	.188
Feeding*Fruit Season	-.132	.132	235.582	-1.006	.316
Resting*Fruit Season	.018	.125	223.743	0.141	.888
Traveling*Fruit Season	.026	.123	215.974	0.210	.834

Table 4.10. Parameter estimates of covariance between standardized values of logged cortisol (ng/g) and behavior with a site interaction.

Parameter	Estimate	Standard Error	df	t-value	Significance
Feeding*Site	-.079	.140	235.600	-0.566	.572
Resting*Site	.072	.127	224.075	0.565	.573
Traveling*Site	-.055	.126	222.386	-.432	.666

Table 4.11. Proposed monthly patterns of energy conservation, maximization, storage, and expenditure in both sites. ↗ indicates a slight increase from the mean; ↘ indicates a slight decrease from the mean; ↑ indicates an increase from the mean; ↓ indicates a decrease from the mean.

Behavior and Cortisol Category	Vatoharanana (Undisturbed) Month	Talatakely (Disturbed) Month	Energy Storage or Extraction	Energy Maximization/ Conservation
Feeding ↑ Cortisol ↑ Resting ↓	Jan 2004[1] Sept-Nov 2004[3] Jan-Mar 2005[1]	Jan-Feb 2004[1]	Extraction	Maximization
Feeding ↑ Cortisol ↓↘ Resting ↓	Feb 2004[1] Apr 2004[2] Dec 2004[1]	Nov-Dec 2004[1]	Storage	Maximization
Feeding ↓ Cortisol ↗ Resting ↑	Jun-July 2004[3]	X	N/A	Conservation
Feeding ↓ Cortisol ↑ Resting ↑	Aug 2004[3]	X	Extraction	Conservation
Feeding ↓ Cortisol ↓ Resting ↑	May 2004	Apr-Sep 2004[2,3] Jan-Feb 2005[1]	N/A	Conservation

[1]December through March are proposed to be energy storage periods by Pereira *et al.,* (1999).
[2]mid-April corresponds to the period when low appetite is initiated in captive groups (Pereira *et al.,* 1990).
[3]June through September are proposed to be energy extraction and conservation periods by Pereira *et al.,* (1999).

Seasonal Cortisol Levels and Behavior

Climate Seasons

Cortisol x Behavior x Temperature: Temperature had a significant effect on the relationship between cortisol and feeding and resting, but not traveling (Table 4.9). Though there was no significant effect of temperature upon fecal cortisol levels (see above), the relationships between cortisol and feeding, and cortisol and resting were stronger during the cool season, and particularly weak during the warm season, as predicted.

Cortisol x Behavior x Temperature x Site: The relationship between fC levels, behavior, and temperature did not differ significantly across sites (Table 4.12), indicating that behavior-fecal cortisol relationships were stronger during the cool season in both sites.

Cortisol x Behavior x Rainfall: The relationship between fC levels and behavior did not vary by rainfall season (Table 4.9), contrary to predictions.

Cortisol x Behavior x Rainfall x Site: The relationship between fC levels, behavior, and rainfall was consistent, and did not differ significantly across sites (Table 4.12), indicating that there was no difference in the relationship between behavior and fC levels across rainfall seasons in these sites.

Ripe Fruit Availability Seasons

Cortisol x Behavior x Fruit: The overall behavioral and physiological responses to changes in fruit availability are depicted in Figure 4.17a. During fruit scarcity cortisol

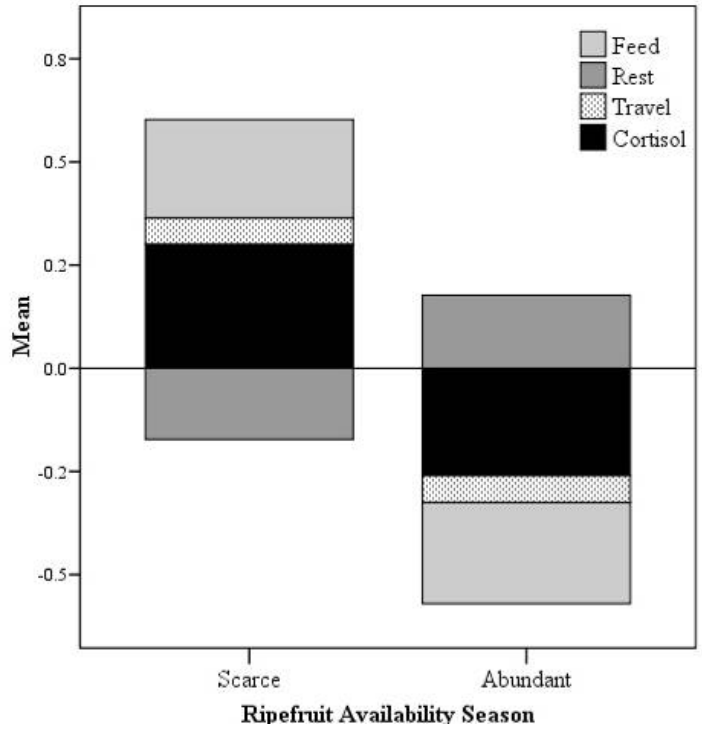
levels and the proportion of time spent feeding and traveling increased, and time spent resting decreased.

The relationship between cortisol and behavior did not vary by ripe fruit availability season. There was no significant interaction effect of any behavior on the relationship between cortisol and ripe fruit season (Table 4.9). These results strongly support the hypothesis that phenology is a better predictor of fC levels than feeding behavior. Furthermore, the only significant individual effect on cortisol levels in all seasonal models (each including site, behavior [either feeding and traveling or resting], and season [either temperature, rainfall, or ripe fruit season]) was ripe fruit availability. Table 4.13 lists significant results from these models.

Cortisol x Behavior x Fruit x Site: The relationship between cortisol levels, behavior, and fruit availability seasons was also consistent across sites, with no significant effects in any of the models (separately run for each behavior), with the exception of the fixed effect ripe fruit availability. There was a significant relationship between ripe fruit availability and fC levels in all models (feeding model: $F(1,73.720)=4.555$, $p=.036$; resting model: $F(1,75.310)=4.579$, $p=.036$; traveling model: $F(1,82.931)=4.109$, $p=.046$), as in the models which excluded site above. The strength of the effect of ripe fruit availability season on the relationship between cortisol and behavior was least subject to modification by site compared with other seasonal parameters (Figure 4.14), indicating that behavior did not effect cortisol levels across ripe fruit availability seasons regardless of other habitat-specific qualities. Figure 4.18 shows patterns of ripe fruit availability, proportion of time feeding, and fecal cortisol levels in each site.

Interestingly, the overall behavioral and physiological response to changes in fruit availability differed across sites. During fruit scarcity in Vatoharanana, energy was mobilized and animals maximized resources by increasing the proportion of time spent feeding and traveling; in contrast, differences across seasons in Talatakely were very slight, and though feeding and cortisol increased during the scarce season, and resting decreased, traveling also decreased (Figure 4.17b). Whereas all independent behavioral and cortisol changes across fruit availability seasons were strong in Vatoharanana, all were weakly associated with fruit availability season in Talatakely, the strongest of which were feeding and traveling (Figure 4.17b), as predicted. Patterns in Vatoharanana appear to have driven the overall pattern reported above (see 'Cortisol x Behavior x Fruit').

(A)



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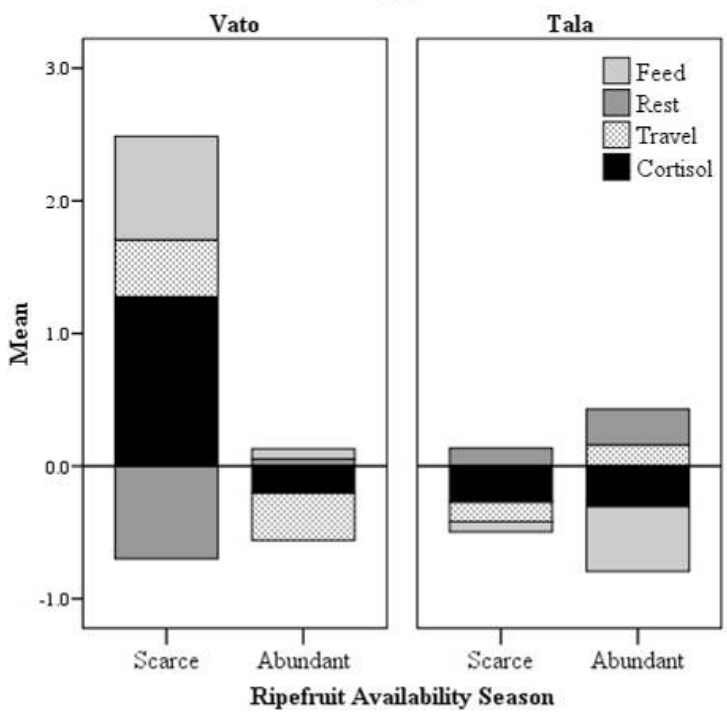

Figure 4.17. Behavioral and physiological response to ripe fruit availability (A) overall and (B) among sites. Cortisol (ng/g) was log-transformed and converted to z-scores.

Table 4.12. Parameter estimates of covariance between standardized values of logged cortisol (ng/g) and behavior, season, and site, with three-way interactions. Models were run for each season-behavior pair separately, with all two- and three-way interactions. Results for each three-way interaction in each model are reported.

(A)

Parameter	**Estimate**	**Standard Error**	**df**	**t-value**	**Significance**
Feeding * Site * Temperature	-.138	.210	221.186	-.656	.512
Resting * Site * Temperature	.117	.183	222.663	.636	.526
Traveling * Site * Temperature	-.204	.185	220.862	-1.101	.272
Feeding * Site * Rainfall	-.356	.194	232.734	-1.834	.068
Resting * Site * Rainfall	.187	.184	221.550	1.014	.311
Traveling * Site * Rainfall	-.086	.200	208.809	-.432	.666
Feeding * Site * Ripe Fruit	.219	.182	232.929	1.205	.229
Resting * Site * Ripe Fruit	-.085	.171	221.140	-.498	.619
Traveling * Site * Ripe Fruit	.015	.176	207.936	.086	.932

Table 4.13. Parameter estimates, standard errors, and significance of covariance between cortisol and behaviors during ripe fruit seasons. A reports significant values from the mixed model including feeding and traveling behaviors; B reports significant values from the mixed model including resting behaviors. Out of all behaviors, temperature, rainfall, and ripe fruit availability seasons, and their interactions, only ripe fruit availability had a significant effect upon fecal cortisol levels.

Parameter	Estimate	Standard Error	df	t-value	Significance
(A) Ripe Fruit	-.496	.162	110.332	-3.050	.003**
(B) Ripe Fruit	-.497	.163	110.249	-3.052	.003**

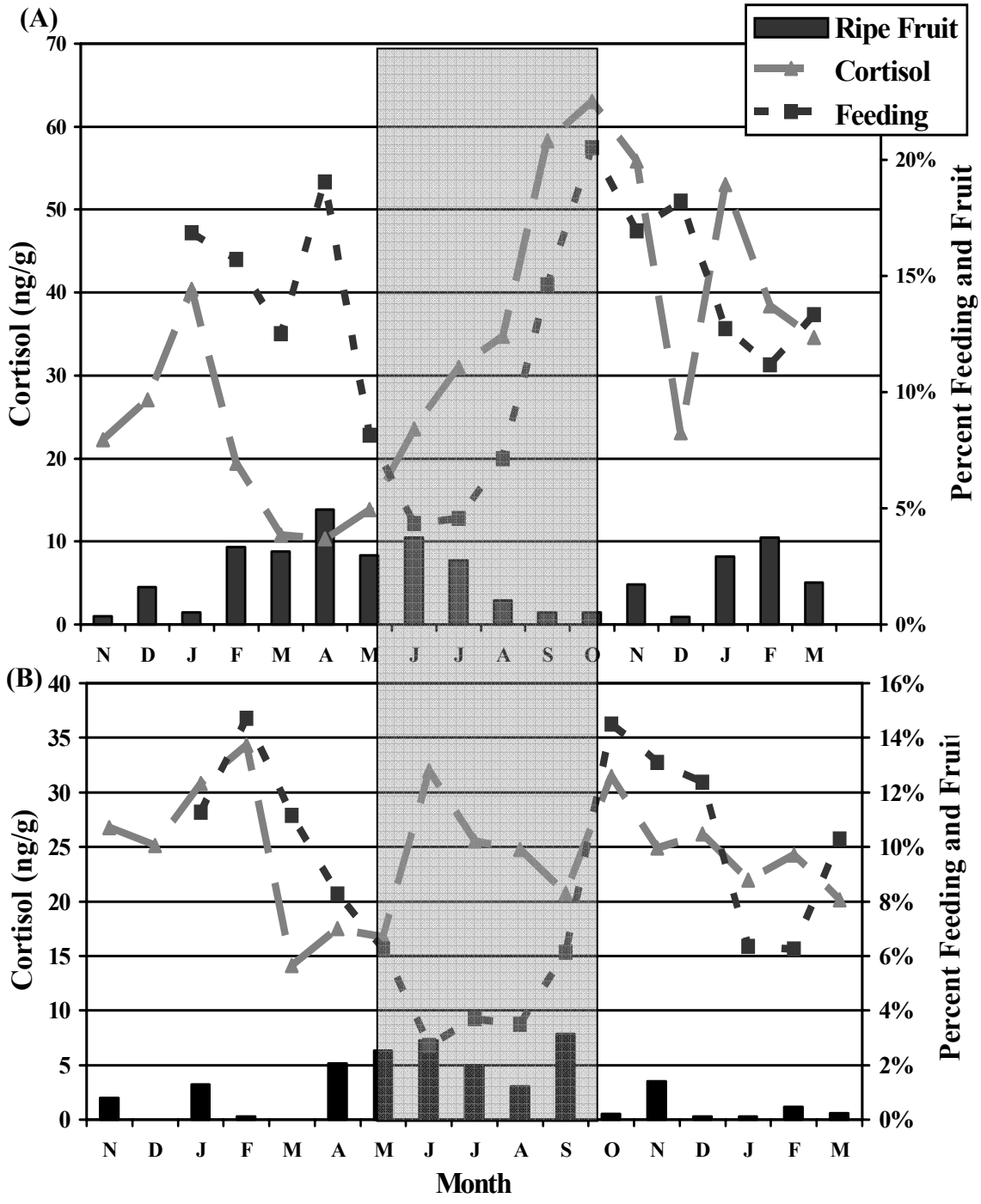

Figure 4.18. Fecal cortisol levels, ripe fruit phenology, and proportion of time feeding in (A) Vatoharanana and (B) Talatakely. Note scale differences. The shaded area indicates gestation which corresponds to the cool/dry season. No infants were born in 2003 or 2005.

Behavior, Ripe Fruit Availability, and Cortisol: The Exceptions

Visual inspection of the association between food and fC levels with ripe fruit phenology determined that in Vatoharanana, the undisturbed site, feeding and fC levels were inversely associated (high proportion of time feeding, low fC levels) when ripe fruit availability was high and animals ingested high quality food (a later peak in feeding with a concurrent trough in cortisol, in December, was likely due to limited sampling that month), indicating that phenology is a better predictor of fC levels than feeding time.

In Talatakely, the disturbed site, feeding and fC levels were inversely related (low proportion of time feeding, high fC levels) two months earlier, when ripe fruit availability was at its lowest (including March, 2004 when ripe fruit was absent) (Figure 4.19). To determine the effect of guava presence upon the relationship between fecal cortisol levels and time spent feeding in the disturbed site, fecal cortisol levels were analyzed with feeding and guava presence or absence, and an interesting relationship emerged. The relationship between cortisol and feeding significantly differed among 'guava seasons', $F(1,225.182)=5.597$, $p=.019$. When guava was absent, cortisol levels and time spent feeding were positively related, as predicted. However, when guava was present, cortisol levels and time spent feeding were inversely related. This may account for the statistically insignificant relationship between overall time spent feeding and cortisol levels reported above.

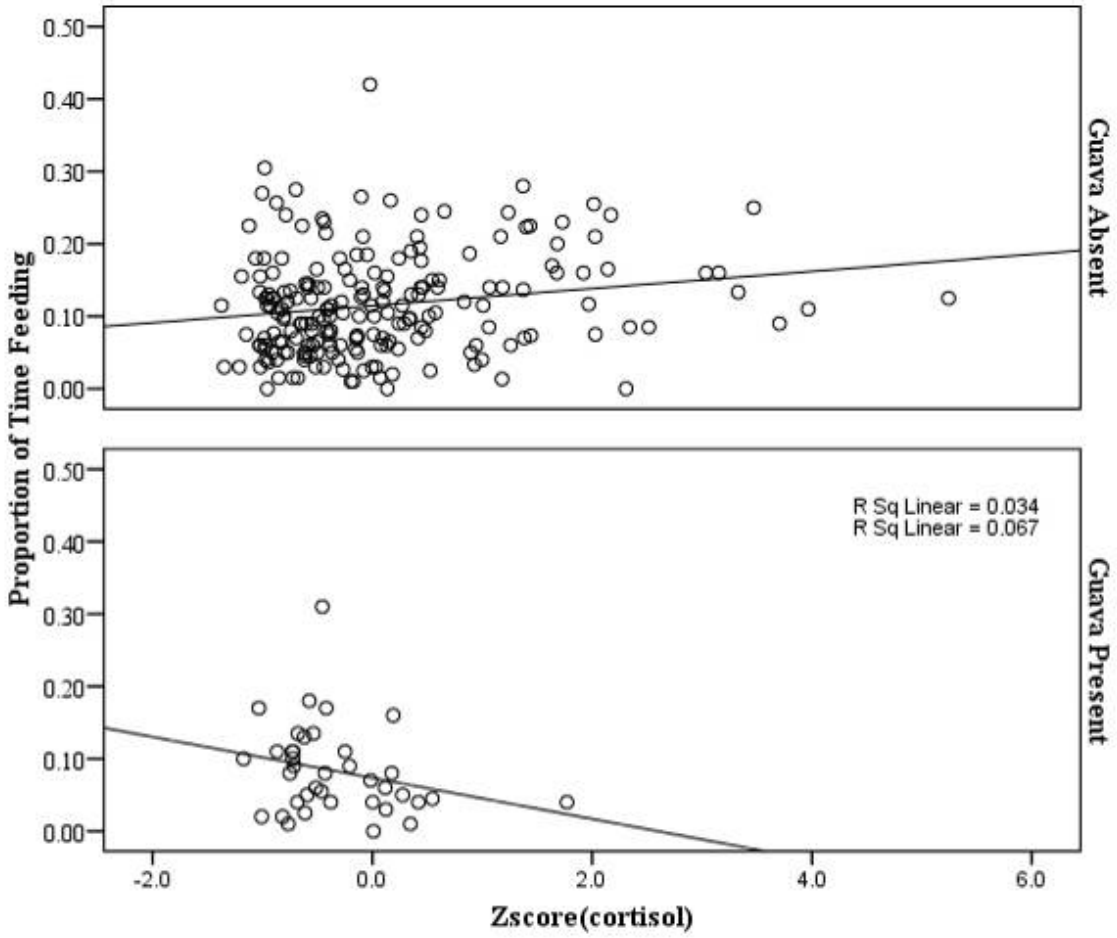

Figure 4.19. Effect of guava presence on the relationship between proportion of time feeding and fecal cortisol excretion. Cortisol levels (ng/g) were standardized. The relationship between cortisol and time feeding was significantly different depending upon whether guava was present or absent, $p<.05$.

DISCUSSION

General Patterns of Cortisol Excretion

Non-invasive field endocrinology is a quantitative, accurate, and reliable tool (Lane, 2006) with which species can be monitored without undergoing additional stress. This study determined that fecal cortisol levels were able to be reliably measured in *Eulemur rubriventer,* a cooperatively breeding, pair-bonded, monogamous species. With the addition of species to the list of those for which we have profiles of cortisol excretion, comparisons can be made to determine if this profile is distinctive compared with non-lemurid primates, or species living in larger groups with different social or mating structures.

Eulemur rubriventer fecal cortisol levels fluctuated throughout the study, with significantly higher levels during dry and ripe fruit scarce seasons. Temperature had no effect on cortisol excretion. Significant correlations, but lack of significant predictive relationships, between cortisol and the proportion of time spent in each behavior indicate that behavior and cortisol act together in response to the environment, but one does not cause the other (but see Astheimer *et al.,* 1992). These relationships did differ throughout the year and among sites. Table 4.11 displays suggested implications of these relationships for energy partitioning throughout the study.

Annual Patterns of Cortisol Excretion

Significantly lower cortisol levels were excreted March through May (the beginning of the austral fall equinox). This was the period just after infants were weaned through breeding, and corresponds with the period when other lemurid species *(Lemur*

catta, Eulemur fulvus rufus) in captivity transition to slower infant growth rates and lose their appetites (Pereira *et al.,* 1999). Lower cortisol levels at this time may result from metabolic adjustments resulting in lower energetic requirements in preparation for winter (Pereira *et al.,* 1999; Ganzhorn *et al.,* 2003b), but this is also a period of food abundance and lower cortisol levels may also be associated with lack of nutritional challenge.

Pre-breeding season fecal cortisol levels may be elevated in primate species where male competition for females is high (Wiebe *et al.,* 1988; Schiml *et al.,* 1996). Similar to *Eulemur rubriventer,* pre-breeding cortisol levels were also lower in muriqui and capuchin males, who are not competitive at this time (Strier *et al.,* 1999; Lynch *et al.,* 2002). Elevated pre-breeding cortisol in *Propithecus verreauxi* males, also coincident with fruit abundance (Fichtel *et al.,* 2007), support the hypothesis that low pre-breeding fecal cortisol levels may characterize species who do not employ male-male mate competition (Strier *et al.,* 1999).

Significantly higher fecal cortisol levels were excreted September through November, as the dry season transitioned from cold to warm. This was the time when all *Eulemur rubriventer* adult females gave birth and all individuals began carrying infants. Fruit availability was decreasing, and the proportion of time feeding was rising and high. This period corresponds with the period when lemurs in captivity regain their appetites and hair and juvenile growth rates increase (Pereira *et al.,* 1999). Pereira *et al.* (1999) stress the importance of flowers, leaves, and unripe fruit in shaping life histories. While fruit scarcity may be challenging, the presence of these alternate food sources will further determine the extent of this response. Despite low ripe fruit availability in Vatoharanana, *Eulemur rubriventer* in that site spent 88.5 – 92% of their time feeding upon ripe fruit,

and a peak in flower bud feeding occurred (Tecot, this study) (Figure 4.20). However, leaf and unripe fruit feeding and presence were negligible and may account for extremely high levels of excreted cortisol. In contrast, groups in Talatakely spent a similar amount of time feeding upon ripe fruit, but flowers were largely unavailable and an increase in leaf eating occurred (Tecot, this study) (Figure 4.21). Cortisol levels peaked in that site as well (though fruit availability was high in September relative to other months in this site, and cortisol peaks occurred one month later, in October). More data are necessary to determine how variable presence of unripe fruits and flowers at this time affect this species, but results from this study indicate that regardless of the presence of alternate food items within the range observed during this study, the absence of ripe fruit elicited fecal cortisol elevations.

Peaks in the proportion of time *Eulemur rubriventer* spent feeding occurred at the end of the year at the start of the austral summer solstice, and correspond with the period characterized by ingestion of 100% of available food in captive lemurs (full appetite) (Pereira *et al.,* 1999). Contrary to the pattern observed in *Eulemur rubriventer* during other periods, cortisol levels declined, indicating that energy storage may occur at this time (increased food intake, low cortisol levels). Metabolic hormones measured in captive lemurs further suggest that energy may be stored between the austral summer solstice and fall equinox (Pereira *et al.*, 1999), which correspond to December through March (warm/wet season) in Madagascar. However, in this study food was not abundant in December, and the relationship between feeding and cortisol levels was variable between January and March.

Though energy was maximized (Tecot, Chapter 3) and the proportion of time spent feeding was high, in both years fecal cortisol levels were elevated and declining between January and March (incidentally seemingly unresponsive to a cyclone in year 1). This may indicate that energy storage was not possible December through February, but was initiated in March when cortisol levels reached their nadir (see below). It is unknown what may cause this pattern, as fruit was rising in abundance in Vatoharanana and was variable in Talatakely, yet the same pattern occurred in both sites. Pride (2005a) reported similar elevations in fecal cortisol in *Lemur catta* at this time, but these elevations were coincident with a decline in rainfall and tamarind fruit availability.

As no apparent response to the cyclone in 2004 was detected, high cortisol levels in this study can not be attributed to the harsh weather. Furthermore, weaning infants cannot explain this pattern, since no infants were born in 2003 to be weaned in early 2004 (Tecot and Overdorff, 2005). Alternatively, high cortisol levels in January and February 2004 and 2005 may be due to different factors: a cyclone in 2004 and weaning in 2005. In fact, five infants were being weaned in 2004, and though aggression is extremely rare in *Eulemur rubriventer,* the majority of aggression observed was associated with weaning (Overdorff and Tecot, 2006). More study is necessary to determine why cortisol levels are elevated at this time of year.

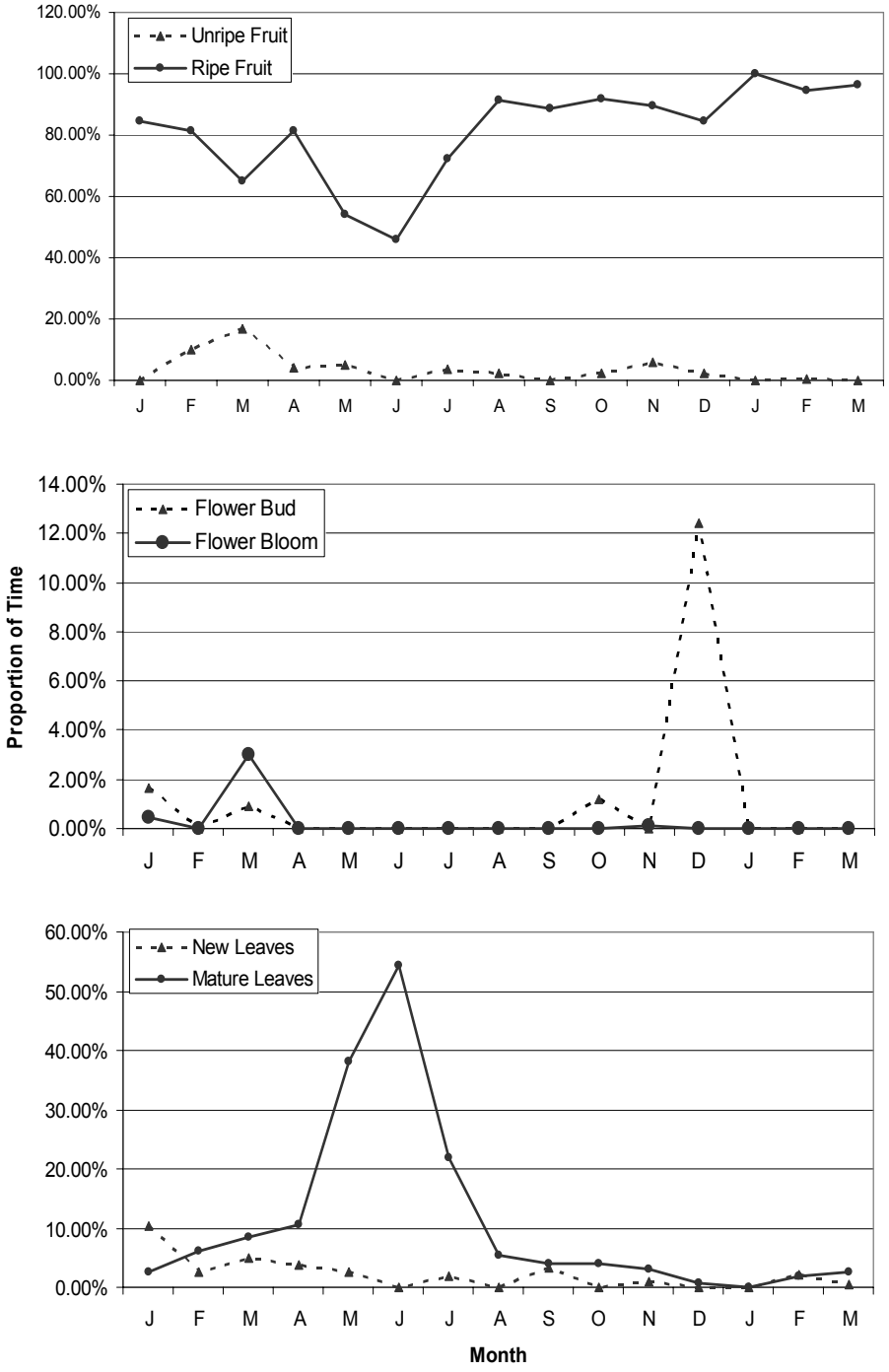

Figure 4.20. Monthly proportion of time spent feeding upon fruit, leaves, and flowers between January, 2004 and March, 2005 in Vatoharanana.

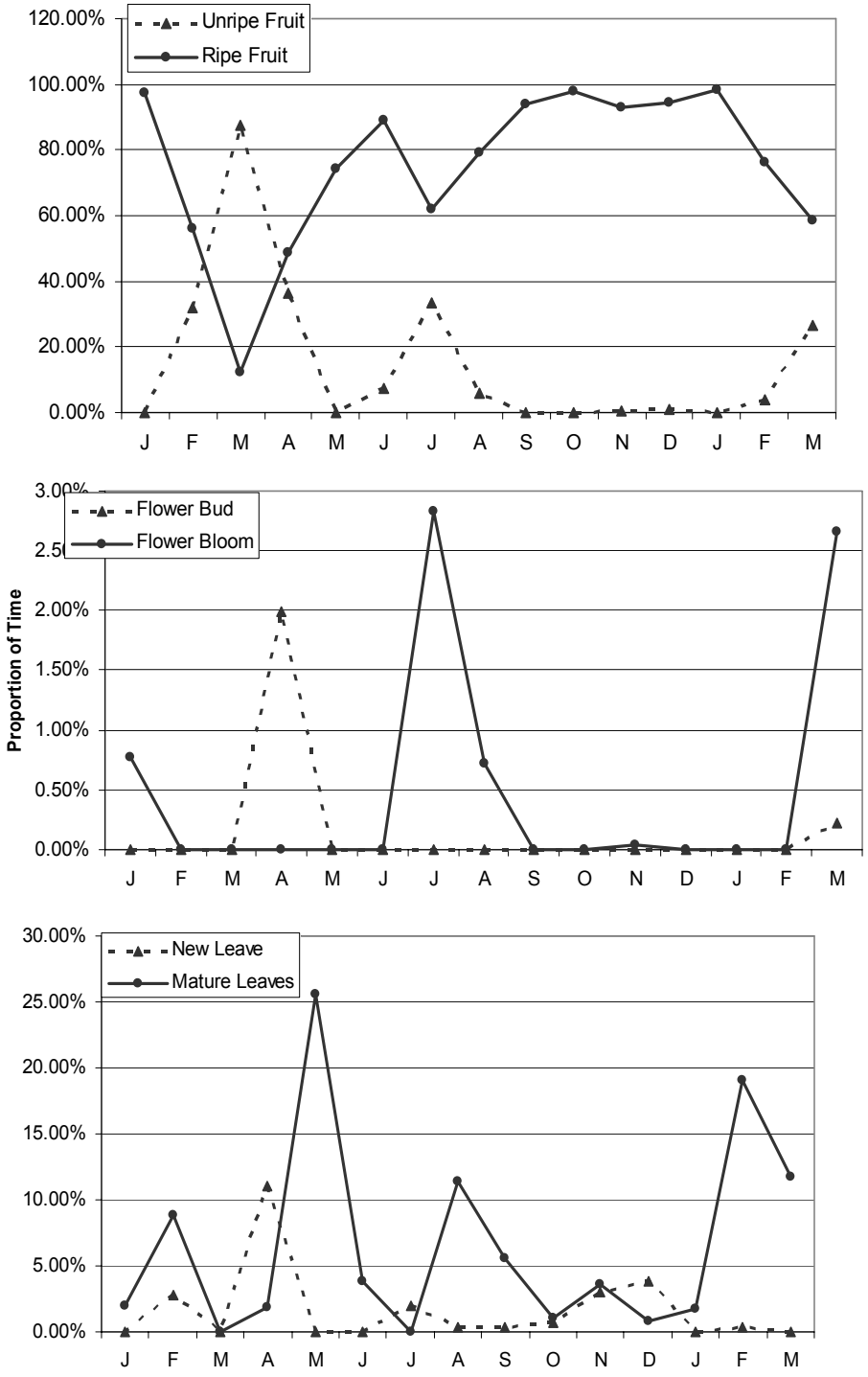

Figure 4.21. Monthly proportion of time spent feeding upon fruit, leaves, and flowers between January, 2004 and March, 2005 in Talatakely.

Cortisol and Climate

Temperature

Tropical species are affected by natural seasonal fluctuations in food availability and climate (van Schaik *et al.*, 1993). Contrary to suggestions that cold weather even in the tropics causes thermoregulatory challenges requiring additional energetic mobilization (see Tecot, Chapter 3), temperature did not affect fecal cortisol levels in this study. Cortisol excretion increased slightly during the cold season, but in general *Eulemur rubriventer* utilized behavioral coping strategies to maintain a thermoneutral state, such as becoming less active (Tecot, Chapter 3) and possibly huddling (Harcourt, 1991; Morland, 1993; Bicca-Marques and Calegaro-Marques, 1998; Nash, 1998; Wright, 1999; Pochron, 2000; Vasey, 2005 Bearder *et al.*, 2006) in cool weather, in support of Morland's (1993) prediction that lemurid responses to temperature change will be largely behavioral, versus physiological. Chacma baboon (Weingrill *et al.,* 2004) cortisol levels rose significantly in winter during coldest temperatures, but these species occupy a large thermal habitat range. Moreover, lower resting metabolic rate in lemurs (Kurland and Pearson, 1986; Snodgrass *et al.,* 2007) may preclude the need for further physiological adjustment in lemurs.

It may be the case that both cool and warm seasons pose different thermoregulatory challenges. The onset of lowered temperatures in Madagascar corresponds with the period when hair growth in captive lemurs is reduced (Pereira *et al.,* 1999), so hair during the warm season is comparatively long and may pose a challenge (*cf* Pereira *et al.,* 1999). However, behavior during the warm season (increased traveling

and feeding, decreased resting) does not appear to support such a suggestion (Tecot, Chapter 3).

Furthermore, captive lemur infants slow growth, appetite and activity decrease, and energy is extracted from adipose tissue during the time corresponding to the cool season in the wild (Pereira *et al.,* 1999). As mentioned above, *Eulemur rubriventer* decrease activity and feed less, and fecal cortisol levels gradually rise throughout the season. Rather than being associated directly with thermoregulation, gradual cool season fecal cortisol excretion may indicate the use of energy stores as one component of an intricate seasonal adaptation.

Alternatively, fecal cortisol elevations may be associated with gestation (Tecot, 2007b). Adult female cortisol levels rise mid-gestation and may be related to the interaction between the placenta and gravid female as the fetal adrenal glands develop (see Ziegler *et al.,* 2004), rather than in response to environmental stress (Tecot, 2007b). Males respond to these elevations with a slightly later mid-gestation cortisol elevation (Tecot, 2007b), which may result in slightly higher cortisol levels during the cool season. Unfortunately, data were only collected during one entire cool season, in which all adult females were pregnant. Since this species tends to reproduce every other year, additional data collected during a cool season which does not coincide with gestation may help explain cool season cortisol elevations.

Precipitation

Rainfall season fecal cortisol levels diverged from expectations, and were higher during the dry season as has also been observed in *Cebus apella nigritus* (Lynch *et al.,* 2002) and *Lemur catta* (Pride, 2005a). While *L. catta* may undergo seasonal water stress

in their environment where dry seasons are prolonged and no rain may fall for several months, *Eulemur rubriventer* in this study live in the eastern rain forests where dry season monthly rainfall totals range from 74-300 mm, with precipitation every month. All observed instances of drinking occurred outside the dry season (Tecot, this study), although drinking frequency is admittedly a questionable indicator of water stress. A better explanation than water stress may be that fecal cortisol levels responded to rainfall because of its large degree of overlap with fruit availability (Strier *et al.,* 1999; Lynch *et al.,* 2002). A lack of variable associations between behavior and fecal cortisol levels across ripe fruit availability seasons overall and in either site, despite significant behavioral changes (Tecot, Chapter 3), support this view. Though not predictably linked year to year (Overdorff and Wright, unpublished data; Wright, 1992; Wright, 2006; Dewar and Richard, 2007), during this study higher precipitation generally accompanied ripe fruit (Tecot, Chapter 2), and there was a significant interaction between rainfall and ripe fruit on fecal cortisol levels which accounted for this variation.

Site differences in the relationships between precipitation and both fruit availability and cortisol levels offer further support for this interpretation. Fruiting and rainfall were significantly related in Vatoharanana but not in Talatakely (Tecot, Chapter 2), indicating that rainfall is a less reliable indicator/cue for *Eulemur rubriventer* fruit availability in the disturbed forest site. In fact, cortisol and rainfall were also significantly related in Vatoharanana but not in Talatakely and suggest that the disruption of climate-plant phenology relationships in disturbed forest may be responsible for a weaker relationship between climate and cortisol. Therefore, the relationship between

cortisol and rainfall observed in this study was the result of the strong relationship between rainfall and fruit phenology.

Cortisol and Fruit Availability

In general, cortisol levels and time spent feeding were positively related, and cortisol levels and food availability were negatively related. Ripe fruit availability was the strongest and most consistent predictor of fecal cortisol levels in the study. These results suggest that periods of ripe fruit scarcity initiate adrenal activation, feeding time increases to mitigate stress during the lean season, and the nutritional status of *Eulemur rubriventer* is indicated by cortisol levels.

These results strongly suggest that primates are limited by the availability of food during periods of food scarcity. Similar results have been found for ring-tailed lemurs (Pride, 2005a), muriquis (Strier *et al.,* 1999), baboons (Sapolsky, 1985), colobus monkeys (Chapman *et al.,* 2007), and chimpanzees (Müller and Wrangham, 2004), though nutritional status was assessed through a variety of measures. For instance, Müller and Wrangham (2004) used percent time feeding as a proxy for food availability, and Chapman *et al.* (2007) used a protein-to-fiber ratio of preferred foods to approximate dietary quality. The absence of a significant predictive relationship between fecal cortisol levels and behavior across ripe fruit availability seasons, and other studies which found behavior to be a less sensitive indicator of stress than cortisol (Coe *et al.,* 1982; Paterson and Pearce, 1992; Schapiro *et al.,* 1993; Clarke *et al.,* 1996; Gust *et al.,* 1996; Smith and French, 1997; Walker *et al.,* 2005) suggest that behavioral measures may not be a good indicator of nutritional stress. Though several measures of food availability are used in primate studies and have met with varying degrees of success in predicting

behavior and population densities (Ganzhorn *et al.,* 2003b), the method employed in this study provided a significant predictive estimate of fecal cortisol levels.

Upon closer inspection of monthly feeding, cortisol, and food availability profiles in this study, there were exceptions to these patterns in both sites. For instance, although ripe fruit was abundant during February and March in Vatoharanana, this was a period of extreme scarcity in Talatakely. In March *no* ripe fruit was available and all Talatakely groups spent 100% of their time feeding upon unripe Chinese guava (*Psidium cattleianum*), an invasive and exotic species not present in Vatoharanana. Although the fruit availability data indicate a severe lean season, and these groups were feeding upon lower quality foods than at other times of the study, time feeding steadily decreased and cortisol levels remained low. In other words, the leanest period during this study was accompanied by the lowest cortisol levels. It appears thus that *Eulemur rubriventer* is able to overcome the stress of the lean season through feeding upon an alternative, introduced food source (but see below). It should be noted, however, that this time of year is the only time in which Talatakely glucocorticoids are higher than those in Vatoharanana.[1] However, this resource may not be sufficient to prepare them for the breeding season (see below), and may even be a false cue: guava may convey the message that food is not limited and animals may consequently miss the environmental cue (scarce resources) initiating behavioral change and sparing energy use.

The other exception to the overall pattern occurred in Vatoharanana. Births occurred in September 2004, indicating that adult females in this site conceived in May. The *only* time during this study when low cortisol and ripe fruit abundance accompanied

a large increase in the proportion of time spent feeding in Vatoharanana was in April 2004, just after the completion of weaning and prior to mating. Weight gain preceding mating has also been reported in ringtailed lemurs *(Lemur catta*) (Pereira, 1993), and Glander and colleagues (1992) reported a seasonal loss of 5-12% in body mass in red-bellied lemurs and red-fronted brown lemurs *(Eulemur fulvus rufus)*, suggesting seasonal fluctuations in weight gain. Increasing food intake during this one month of abundance and very low stress indicates that *Eulemur rubriventer* schedules reproduction with resource availability: for adult females, April is a month of recovery from weaning and preparing for winter and mating; for newly independent infants it is a time of ample provisions and a "head start on life" (Wright, 1999, p. 56).

Overdorff *et al.,* (1999) also found reproductive scheduling with fruit availability to be of great importance to infant survivorship. *E. f. rufus* infant survivorship in Ranomafana was higher when food abundance was coincident with late lactation/early weaning, rather than mid-gestation (Overdorff *et al.,* 1999). In *E. rubriventer*, extremely scarce resources in Talatakely during weaning, just prior to and coincident with 100% guava feeding, may explain why this same relationship between cortisol, resource abundance, and feeding time was not present in this site. Furthermore, insufficient energy during this critical time may explain the very late births which occurred in that site. For instance, reproductive timing in many vertebrate species may depend upon the energetic condition of a female (Lichtenbelt, 1993); energetic stress can suppress reproduction to conserve reproductive effort when the environment is unfavorable (Brockman and van Schaik, 2005). These highly opportunistic breeders (May and

Rubenstein, 1985) adopt a facultative reproductive strategy (Negus and Berger 1972), and have been termed classical breeders (*birds* Drent and Daan, 1980) and/or capital breeders (*plants and animals* Jönsson, 1997; *primates* van Schaik and van Noordwijk, 1985) because they may take advantage of food abundant periods by storing nutrients (Richard *et al.*, 2000), and breed once they reach high enough stores for successful reproduction.

Thus, while food scarcity imposes strong selective pressure via prolonged increased cortisol levels, the degree of pressure may depend upon the abundance and quality of food during the abundant season. Several studies have reported increased competition during the abundant season (Sauther, 1993; Overdorff *et al.,* 1999), and in deciduous forest, population densities are reportedly limited by abundant-season food availability (Ganzhorn *et al.,* 2003b). Selection likely acts on the ability to store energy during abundant seasons because of the subsequent impact on surviving food-scarce seasons.

If *Eulemur rubriventer* are capital breeders, or relaxed income breeders (Brockman and van Schaik, 2005; see Tecot, Chapter 1) where there is some combination of endogenous and exogenous cuing, individuals in Talatakely may wait to breed until energy stores are sufficient. This likely occurred well into the typical peak gestation period, and thus births occurred in November, January, and March, versus end of August through October when births typically peak (Tecot and Overdorff, 2005; Tecot, personal observation). (Consequently these results also indicate a longer, more flexible, or more frequent conceptive period than suggested for wild diurnal/cathemeral lemurs [Richard and Dewar, 1991; Brockman and Whitten, 1996; Wright, 1999; Whitten and Brockman,

2001; Blanco, *accepted*]). Thus, resource abundance may be required to some extent during *both* the late-lactation/weaning period (Lack, 1950; Altmann, 1980; van Schaik and van Noordwijk, 1985; Bronson, 1995; Wright, 1999; Di Bitetti and Janson, 2000) *and* the pre-breeding period, while births occur during lean periods (Tecot, personal observation). Such out of season births would likely not confer an advantage upon adult females or their infants. Although both adult males (Overdorff and Tecot, 2006) and juveniles (Tecot and Overdorff, 2005; Tecot, 2007b; Ziegler and Tecot, 2007) carry infants extensively, help may be limited during severe resource depressions when energy intake is minimal. While plasticity enables species to respond to environmental changes (Reed *et al.,* 2006), results from this study implicate the actions of stabilizing selection against females who diverge from the breadth of *population-wide* reproductive schedules.

Alternatively, the strategy of relying upon energy stores during the pre-breeding season may be confined to Talatakely, where additional unpredictability may occur (Tecot, Chapter 2). In this study the main peak in fruiting occurred in February (Vatoharanana; peaks were not discernible in Talatakely) and remained elevated through June (see Chapter 2, Figure 2.21), through the breeding season. However, April though July or August is typically a lean period in Ranomafana, specifically Vatoharanana (Meyers and Wright, 1993; Overdorff, 1991, 1992, 1993ab; Hemingway, 1996, 1998; Balko, 1998; Overdorff and Wright, unpublished manuscript). Thus, animals in Vatoharanana may not rely upon food abundance during the pre-breeding season (although multiple-year research should clarify the frequency of this pattern and its relationship with reproduction). Inter-annual variability in rainfall may impact fruiting similarly (Atsalis, 1999a; Hemingway, 1996; Sørg and Røhner, 1996), but in Talatakely

climate and rainfall are not clearly aligned (Tecot, Chapter 2). Therefore, pre-breeding fruit abundance may only be critical for reproduction in the disturbed population.

Habitat Quality

Although cortisol levels did fluctuate in response to food availability, and site differences were apparent, not all predictions associated with site differences were supported. While overall patterns were similar as predicted, contrary to expectations, the undisturbed forest (Vatoharanana) population in this study excreted higher levels of cortisol than disturbed forest (Talatakely) populations. The magnitudes of peaks were greater and, though variable, the duration of peaks tended to be longer in Vatoharanana. When comparing populations, elevated cortisol levels are typically assumed to indicate a poorer quality and more stressful habitat (Wingfield and Romero, 2001). In fact, mean cortisol levels in black howler monkey (Martinez-Mota *et al.,* 2007) and red colobus monkey (Chapman *et al.,* 2006) fragmented forest populations were lower than those in intact forest. *Lemur catta* in seasonally dry forest did not respond at all to food fluctuations, but those subject to a harsh, dry climate excreted higher cortisol levels (Cavigelli, 1999). In contrast, the only time when fecal cortisol levels were higher in Talatakely was during the abundant season, yet this was mainly due to extremely low levels in Vatoharanana since Talatakely levels were at their nadir.

Among mammals, a long-term study comparing populations of bighorn sheep found that ewes in the more disturbed site (more roads and oil wells) had lower cortisol levels than those in a less disturbed site (Sayre, 1996). Rather than accepting the found relationship that species in undisturbed sites may have higher fecal concentrations of cortisol than those in disturbed sites, Sayre (1996) suggested that the undisturbed site was

in reality more disturbed, and the disturbed site actually afforded the ewes several benefits. This is puzzling, since the same study reported modifications in behavior in response to well maintenance and a 50% decline in population size in the disturbed site, but perhaps if energetic intake was not affected cortisol levels would not increase.

Conversely, it is proposed here that, when comparing populations, higher mean cortisol values in one population are not directly indicative of heightened energetic challenge, or stress. For instance, Talatakely cortisol levels did vary seasonally, but only slightly, particularly when compared with cortisol level fluctuations in Vatoharanana. Differences among sites during climate and fruit availability seasons indicated that during times when cortisol levels were highest (*e.g.,* dry and ripe fruit scarcity seasons), fecal cortisol levels in Vatoharanana, the undisturbed forest, were significantly higher; when cortisol levels were lowest (*e.g.,* wet and ripe fruit abundance seasons), fC levels were either not significantly different among sites, or tended to be higher in Talatakely, the disturbed forest. The results from this study suggest that during times of challenge only groups in Vatoharanana were able to launch a full response.

Though these results conflict with what is generally expected when comparing disturbed and undisturbed habitats, studies of birds and salamanders have yielded similar results (*e.g.,* Homan *et al.,* 2003; Cyr and Romero, 2007). Taken together, these studies suggest that populations living in more disturbed sites may have *lower* corticoid levels than populations living in relatively undisturbed sites either due to the inability to launch a full physiological response, or due to tolerance or habituation to the stressor (Nisbet, 2000; Homan *et al.,* 2003; Romero, 2004).

Resources are scarcer in Talatakely and fruit availability is unpredictable month to month (Tecot, Chapter 2) and supra-annually (Wright, 1999; Overdorff and Wright, unpublished manuscript). While guava alleviated some of the food stress brought on by ripe fruit scarcity (see above), the weak response to food scarcity in Talatakely in general remains unexplained by the hypothesis that food scarcity initiates changes in behavior and cortisol. Since the stressor in this case is an unpredictable resource base and behavioral responses were also slight in this population (Tecot, Chapter 3), it appears that energetic storage or resource maximization strategies are not employed. Therefore, it is unlikely that these animals have managed to cope with the stress of unpredictable food and are thus likely chronically stressed.

It is suggested here that Talatakely lemurs are not able to respond to such stressors through prolonged changes in behavior and hormones. Narrower peaks in cortisol excretion suggest that the Talatakely population may employ a strategy whereby glucocorticoids are only mobilized (and hence behavior changed) during the most intensive periods (*e.g.,* at the height of fruit scarcity), and are not sustained for the duration of the challenge. *E. rubriventer* can then avoid sustained elevations in glucocorticoid levels throughout the entirety of the adverse conditions, and thus avoid the detrimental fitness effects of long-term exposure (*e.g.,* inhibited reproduction and immune function) (Sapolsky, 1987). This response is similar to that found by Hennessey and colleagues (1995) in which primates regularly exposed to social and environmental novelty experienced relatively lower adrenal sensitivity than those with more stable lifestyles.

Additionally, changes in food availability may occur *too* frequently and unpredictably for *E. rubriventer* or other lemur species to receive seasonal, honest cues from the environment about when food will be abundant or scarce, in contrast with capital breeders (Jönsson, 1997; van Schaik and van Noordwijk, 1985), preventing them from storing energy during the abundant season (see Brockman and van Schaik, 2005 and Tecot, Chapter 1), and suffering during the scarce season. Alternatively, rapid fluctuations in ripe fruit availability in the disturbed habitat raise the possibility that cortisol levels fluctuate at a rapid rate as well. In such a situation, biweekly averages may be a muted representation of the actual response.

Reproductive Success

Evidence for an inability to respond appropriately to the environment comes from reproduction data collected during this study. When energy in the environment is minimal, and energy is not stored, reproduction will not be supported to the extent that it is in animals with a healthy energy supply. For instance, Overdorff *et al.* (1999) report that red-fronted brown lemur infant survivorship is lower in females who weigh less, and stressed individuals may experience inhibited reproduction (Wasser and Starling, 1988; Mendoza and Mason, 1988; Chatterton *et al.,* 1991; Sapolsky, 1992; Cameron, 1997; Bronson, 1999). Furthermore, chronically stressed European starlings, with lower baseline levels of cortisol compared with unstressed individuals, experienced reduced reproductive success (Cyr and Romero, 2007). All adult female *E. rubriventer* in this study produced offspring, but three of seven births occurred outside of the normal birth peak. As mentioned above, all of these occurred in Talatakely. Relaxed breeding seasonality may indicate a particularly resource-rich year (Daan and Tinbergen, 1997;

Brockman and van Schaik, 2005; see Tecot, Chapter 1), and low cortisol levels and small changes in feeding behavior throughout the study relative to lemurs in Vatoharanana may corroborate such an interpretation. However, each of these out of season births resulted in mortality within 2.5 months (Tecot and Overdorff, 2005). With the above proposed pre-breeding energetic sink, these results suggest the exertion of strong environmental pressures on reproduction, and suggest either a relaxed income or capital breeding strategy (*cf* Brockman and van Schaik, 2005) whereby individuals are responsive to endogenous cues.

Furthermore, *Eulemur rubriventer* in Talatakely and Vatoharanana appear to have an interbirth interval of approximately 2 years (Tecot and Overdorff, 2005; Tecot, personal observation). Mean interbirth intervals have been calculated for two other sympatric species in Ranomafana National Park; *Eulemur fulvus rufus*, the closest relative to *Eulemur rubriventer* in this forest, has a mean interbirth interval between surviving infants of 18.6 months (Overdorff *et al.,* 1999), and *Propithecus edwardsi* has a mean interbirth interval of 18 months (Pochron *et al.,* 2004). Interbirth intervals also decreased when a female's infant died (Tecot, personal observation), as did those in *Propithecus edwardsi* (Pochron *et al.,* 2004). These results suggest that these species may have adopted a strategy of "bet hedging" (*cf* Stearns, 1976; Richard *et al.,* 2002; Pochron *et al.,* 2004), saving reproductive effort for times when the environmental conditions are optimal. Such a strategy is often observed in species living in unpredictable habitats, and several authors assert that this strategy has been selected for by Madagascar's harsh and unpredictable environment (*e.g.,* Wright, 1999; Richard *et al.,* 2002; Pochron *et al.,* 2004).

Another model which may explain delayed reproduction is termed the Emergency Life History Stage (ELHS; see Wingfield *et al.,* 1998). This states that when unpredictable events occur, the progression of life history cycles may be suspended while behavioral and physiological modifications occur to help an animal survive. Once this emergency has abated the animal will either resume the life history stage it was in prior to the emergency or, if the event is extended, begin the life history stage appropriate for that particular time (Wingfield *et al.,* 1998; Wingfield and Kitaysky, 2002; Wingfield, 2003). Reproductive data in this study fit the ELHS model well, but further research is required to adequately test this.

Longer-term and more detailed data on *Eulemur rubriventer* reproduction, particularly infant mortality, interbirth intervals, and the likelihood of conception during different resource seasons and following births, are needed to further evaluate environmental influences upon reproductive success. Comparisons of cortisol levels and reproductive schedules with sympatric primates will inform on the different strategies employed in response to the same ecological conditions. Such "evolutionary ecology" (Whitten, 2000) studies can help explain species-specific social and mating systems. Moreover, hormonal profiles of Malagasy primates will provide a basis for comparison with primates from other regions not subject to Madagascar's unique environment, and contribute to understanding the relationship between the environment and hormonal profiles.

To fully determine whether lower baseline cortisol levels in the disturbed habitat are due to chronic stress, the acute response to stressors should be investigated. If the HPA axis is able to launch a substantial response to stress, this dampened response may

not be attributable to chronic stress, but rather habituation. It is not likely that lower levels correspond to periods of greater food availability than is assumed in this study, as extensive phenological and habitat assessments were made during this study which supported results found during previous studies conducted in these sites.

CONCLUSIONS

In conclusion, climate had a negligible influence upon *Eulemur rubriventer,* despite strong inter-annual unpredictability in rainfall which is proposed to have strongly contributed to the unique traits of lemurs (Dewar and Richard, 2007). However, rainfall did exert pressure upon this species insofar as it is related to fruit availability (see Wright, 2006 and Dewar and Richard, 2007), and these results support models of lemurid evolution which suggest that inter-annual unpredictability in climate influences inter-annual unpredictability in food resources, which require special adaptations (Wright, 1999, 2006; Dewar and Richard, 2007). Longer-term data will better inform on the impact of inter-annual variation in rainfall and plant phenology upon lemur cortisol levels.

Perhaps most interesting is the impact of habitat disturbance upon the relationship between precipitation, fruiting, and cortisol. There is a strong relationship between rainfall and fruiting phenology in Madagascar (Hemingway, 1996; Sørg and Røhner, 1996; Atsalis, 1999a; Tecot, Chapter 2; but see Overdorff and Wright, unpublished manuscript). Lemurs as a clade have likely adapted to inter-annual unpredictability, and part of this process was likely made possible by the reliable relationship between climate and plant reproduction (Wright, 2006; Dewar and Richard, 2007). Habitat disturbance may disrupt this relationship such that rainfall is not a reliable cue of fruit availability,

and lemur cortisol levels respond to more immediate signals such as the actual presence of fruit. By removing reliable photoperiodic and climatic cues, habitat disturbance appears to have introduced a more unpredictable environment to which lemurs have not yet adapted. It should be noted, however, that the positive relationship between fruiting phenology and rainfall in Madagascar is not a hard and fast rule (Overdorff and Wright, unpublished manuscript), and determining the frequency with which these variables diverge may provide important data on the different levels of unpredictability these animals experience.

The availability of ripe fruit had the strongest effect upon fecal cortisol levels in *Eulemur rubriventer*, and fecal cortisol levels elevated when food was scarce. Because fruit may be scarce up to 6 months out of the year in Madagascar (Wright *et al.,* 2005), fecal cortisol elevations may be more prolonged in lemurs than other frugivorous primates living in other habitats with shorter fruit-scarce periods. Fecal cortisol levels may become elevated when feeding effort increases, though this relationship may reverse, for example during periods of energy storage prior to the mating season. Future studies of the hormonal correlates of seasonal variation should take care to collect detailed phenological data to enable closer inspection of the dynamic relationship between organisms and the environment, and facilitate investigations of energy maximization, conservation, storage, and extraction strategies.

The fruiting of guava, though an introduced species, appears perfectly timed with fruit scarcity to sustain *Eulemur rubriventer* through the lean season preceding mating, as indicated by very low cortisol levels and a low proportion of time spent feeding. However, later births in Talatakely, the disturbed site, suggest that unripe fruit provided

by *Psidium cattleianum* prior to the mating season may not be sufficient to overcome the patchy temporal distribution of fruit in Talatakely, and promote reproduction.

Although regenerating, resources in Talatakely may not be predictable enough to sustain large populations. In fact, the populations of *Propithecus edwardsi, Eulemur fulvus rufus,* and *Prolemur simus* in this site have recently undergone drastic reductions in size (Wright, personal communication). The manner in which food availability imparts selective pressure upon reproduction, for instance pre- or post-conception, remains unknown. Continued studies of stress may include measures of reactivity to determine the ability of animals to respond to acute stress. Moreover, data on fetal loss and reproductive hormones may help further explain reproductive strategies in this species, such as twinning and long inter-birth intervals.

Fecal cortisol levels were only higher in the disturbed site in the absence of any significant challenge. During times of challenge, the undisturbed forest population launched strong behavioral and hormonal responses. It is suggested that the disturbed forest population is unable to sustain high glucocorticoid levels for the duration of a challenge, and may adopt a different strategy whereby they only respond at the height of a challenge, when energy mobilization is critical to survival.

Relative to each other, groups in Talatakely adopted an energy conservation strategy and those in Vatoharanana adopted an energy maximization strategy (Tecot, Chapter 3). When resources are scarce, increased time resting may be the only available energetic adjustment option when animals are forced to feed less (*cf* Nash, 1998) and a *time/energy expenditure minimizing strategy* is adopted. A time budget which maximizes energy relative to another time budget (which necessarily minimizes energy expenditure)

may indicate energy storage versus merely filling current energy requirements (Hemingway, 1999). Together with results from this study, the energetic strategy utilized by groups in Talatakely appears to be the result of living in an environment with more limited energy and energetic storage opportunities than Vatoharanana. Vatoharanana groups are more flexible, able to partition energy to cope with energetic challenges as they arise.

Finally, the results of this study have implications for conservation management (Wasser *et al.,* 1997; Cockrem, 2005; Walker *et al.,* 2005; Keay *et al.,* 2006). *Eulemur rubriventer* are at high risk of extinction and are listed as 'vulnerable' on the IUCN Red List (IUCN, 2006). Infant mortality has been estimated to reach as high as 50% (Mittermeier *et al.*, 2006). As mentioned above, population numbers of sympatric species in Talatakely are dwindling (Wright, personal communication), and management decisions in the near future may be crucial to the survival of the Talatakely *Eulemur rubriventer* population. It is exceedingly important to recognize that low levels of cortisol do not necessarily indicate a stress-free state. On the contrary, individuals with a substantial stress response may be best equipped to deal with stressors, such as new environments brought on by translocations. Furthermore, elevated cortisol levels associated with ripe fruit scarcity confirm that ripe fruit is an essential component to this species' diet, regardless of other food items available in the environment. Unripe fruit may sustain them through the scarce season, though it is not certain if a diet of unripe fruit can support reproduction. Therefore, assessments of this species' habitat, or any attempt to ameliorate the impact of deforestation, should focus upon adequate and regular access to fruit-bearing resources, particularly those which provide ripe fruit during scarce

seasons and enable energy storage. Lastly, the situation in Talatakely may be critical. Population declines may be predicted by cortisol levels (Chapman *et al.,* 2007) because of their impact upon reproduction (Sapolsky, 1985, 1992; Wasser and Starling, 1988; Mendoza and Mason, 1988; Chatterton *et al.,* 1991; Arnold and Dittami, 1997; Cameron, 1997; Bronson, 1999), immune function (Cohen, 1988; Esch *et al.,* 1975; Keller *et al.,* 1983; Laudenslager *et al.,* 1983; Muehlenbein, 2006), mortality (Colwell *et al.,* 1988; Rodway *et al.,* 1996; Cotter and Gratto, 1995; Pride, 2005b), and longevity (Burrows *et al.,* 1994). A severely muted hormonal and behavioral response to known environmental challenges, coupled with a high rate of infant mortality (Mittermeier *et al.,* 2006; Tecot, this study), indicates that this population may be at risk of declining.

References

Abbott, D.H., Saltzman, W., Schultz-Darken, N.J., Tannenbaum, P.L. 1998. Adaptations to subordinate status in female marmoset monkeys. *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology*. 119(3):261-274.

Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Beanjevic, M., Garland Jr., T., Sapolsky, R.M. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*. 43:67-82.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: B.N. Petrov and F. Caski, editors. *Proceedings of the Second International Symposium on Information Theory*. Akademiai Kiado, Budapest. Pp. 267–281.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*. 49:227-267.

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Amirat, Z., Khammar, F., Brudieux, R. 1980. Seasonal changes in plasma and adrenal concentrations of cortisol, corticosterone, aldosterone, and electrolytes in the adult male sand rat (*Psammomys obesus*). *General and Comparative Endocrinology*. 40(1):36-43.

Arnold, W. and Dittami, J. 1997. Reproductive suppression in male alpine marmots. *Animal Behaviour*. 53(1):53-66.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scandinavica*. 23:355–365.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C. 1995. Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior*. 29:442-457.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Bales, K.L., French, J.A., Hostetler, C.M., Dietz, J.M. 2005. Social and reproductive factors affecting cortisol levels in wild female Golden Lion Tamarins *(Leontopithecus rosalia)*. *American Journal of Primatology*. 67:25–35.

Balko, E.A. 1998. *A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by* Varecia variegata variegata *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Syracuse, NY: SUNY-CESF. 245 p.

Bercovitch, F.B. 1992. Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior*. 26:272-282.

Bercovitch, F.B. and Ziegler, T.E. 2002. Current topics in primate socioendocrinology. *Annual Review in Anthropology*. 31:45-67.

Bicca-Marques, J.C. 2003. How do howler monkeys cope with habitat fragmentation? In: L.K. Marsh, editor. *Primates in Fragments: Ecology and Conservation*. New York: Kluwer. Pp. 283-303.

Blanco, M. *In Press*. Reproductive schedules of brown mouse lemurs *(Microcebus rufus)* at Ranomafana National Park, Madagascar. *International Journal of Primatology*.

Breuner, C.W., Wingfield, J.C., Romero, L.M. 1999. Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *Journal of Experimental Zoology*. 284(3):334-342.

Brockman, D.K. 1994. *Reproduction and mating system of Verreaux's sifaka, Propithecus verreauxi, at Beza Mahafaly, Madagascar*. New Haven, CT: Yale University.

Brockman, D.K. and van Schaik, C.P. 2005. Seasonality and reproductive function. In: D.K. Brockman, C.P. van Schaik and M.A. van Noordwijk, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 269-305.

Brockman, D.K. and Whitten, P.L. 1996. Reproduction in free-ranging *Propithecus verreauxi:* estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology*. 100:57-69.

Brockman, D.K., Whitten, P.L., Richard, A.F., Schneider, A. 1998. Reproduction in free-ranging male *Propithecus verreauxi*: Hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*. 105:137-151.

Brockman, D.K., Meltz, K., Whitten, P.L. 2003. Noninvasive assessments of stress in male sifaka *(Propithecus verreauxi)*. *American Journal of Physical Anthropology*. S36:72.

Brockman, D.K., Whitten, P.L., Richard, A.F. 2000. Birth season cortisol levels in dispersing male *Propithecus verreauxi*. *American Journal of Physical Anthropology*. S30:112-113.

Bronson, F.H. 1995. Seasonal variation in human reproduction: Environmental factors. *The Quarterly Review of Biology*. 70(2):141-164.

Bronson, F.H. 1999. Puberty and energy reserves: a walk on the wild side. In: K. Wallen and J. E. Schneider, editors. *Reproduction in Context*. Cambridge: MIT Press. Pp. 15-34.

Buck, C.L., O'Reilly, K.M., Kildaw, S.D. 2007. Interannual variability of Black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *General and Comparative Endocrinology*. 150(3):430-436.

Budnitz, N. and Dainis, K. 1975. *Lemur catta*: Ecology and Behavior. In: I. Tattersalll and R. W. Sussman, editors. *Lemur biology*. New York: Plenum. Pp. 219–236.

Burrows, R., Hofer, H., East, M.L. 1994. Demography, extinction and intervention in a small population: The case of the Serengeti wild dogs. *Proceedings of the Royal Society of London Series B*. 256:281-292.

Cameron, J.L. 1997. Stress and behaviorally induced reproductive dysfunction in primates. *Seminars in Reproductive Endocrinology*. 15(1):37-45.

Carlstead, K., Brown, J.L., Monfort, S.L., Killens, R., Wildt, D.E. 1992. Urinary monitoring of adrenal responses to psychological stressors in domestic and nondomestic felids. *Zoo Biology*. 11(3):165-176.

Carlstead, K. and Brown, J.L. 2005. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black *(Diceros bicornis)* and white *(Ceratotherium simum)* rhinoceros. *Zoo Biology*. 24(3):215-232.

Cavigelli, S.A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*. 57(4):935-944.

Cavigelli, S.A., Dubovick, T., Levash, W., Jolly, A., Pitts, A. 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs *(Lemur catta)*. *Hormones and Behavior*. 43:166–179.

Cavigelli, S.A., Monfort, S.L., Whitney, T.K., Mechref, Y.S., Novotny, M., McClintock, M.K. 2005. Frequent serial fecal corticoid measures from rats reflect circadian and ovarian corticosterone rhythms. *Journal of Endocrinology*. 184(1):153-163.

Chamove, A.S. and Bowman, R.E. 1978. Rhesus plasma cortisol response at four dominance positions. *Aggressive Behavior*. 4:43-55.

Champoux, M., Zanker, D., Levine, S. 1993. Food search demand effort effects on behavior and cortisol in adult female squirrel monkeys. *Physiology and Behavior*. 54:1091-1097.

Chapman, C.A., Saj, T.L., Snaith, T.V. 2007. Temporal dynamics of nutrition, parasitism, and stress in Colobus monkeys: Implications for population regulation and conservation. *American Journal of Physical Anthropology*. 134(2):240-250.

Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.L., Saj, T.L., Ziegler, T.E. 2006. Do food availability, parasitism, and stress have synergistic effects on Red Colobus populations living in forest fragments? *American Journal of Physical Anthropology*. 131:525-534.

Charnov, E.L. and Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology*. 1(6):191-194.

Chatterton, R.T., Kazer, R.R., Rebar, R.W. 1991. Depletion of luteal phase serum progesterone during constant infusion of cortisol phosphate in the cynomolgus monkey. *Fertility and Sterility*. 56:547-554.

Chrousos, G.P., Torpy, D.J., Gold, P.W. 1998. Interactions between the hypothalamic-pituitary-adrenal axis and the female reproductive system: Clinical implications. *Annals of Internal Medicine*. 129:229-240.

Clarke, M.R., Harrison, R.M., Didier, E.S. 1996. Behavioral, immunological, and hormonal responses associated with social change in rhesus monkeys *(Macaca mulatta)*. *American Journal of Primatology*. 39:223-233.

Cockrem, J.F. 2005. Conservation and behavioral neuroendocrinology. *Hormones and Behavior*. 48(4):492-501.

Coe, C.L., Franklin, D., Smit, E.R., Levine, S. 1982. Hormonal responses accompanying fear and agitation in the squirrel monkey. *Physiology and Behavior*. 29:1051-1057.

Coe, C.L. and Levine, S. 1995. Diurnal and annual variation of adrenocortical activity in the squirrel monkey. *American Journal of Primatology*. 35:283-292.

Coe, C.L. and Scheffler, J. 1989. Utility of immune measures for evaluating psychological well-being in nonhuman primates. *Zoo Biology*. 1:89-99.

Cohen, S. 1988. Psychosocial models of the role of social support in the etiology of physical disease. *Health Psychology*. 7:269-297.

Colwell, M.A., Gratto, C.L., Oring, L.W., Fivizzani, A.J. 1988. Effects of blood sampling on shorebirds: Injuries, return rates and clutch desertions. *Condor*. 90:942-945.

Cook, C.J., Mellor, D.J., Harris, P.J., Ingram, J.R., Matthews, L.R. 2000. Hands-on and hands-off measurement of stress. In: G.P. Moberg and J.A. Mench, editors. *The Biology of Animal Stress*. New York: CABI Publishing. Pp. 123–146.

Coop, R.L. and Holmes, P.H. 1996. Nutrition and parasite interaction. *International Journal of Parasitology*. 26:951-962.

Cotter, R.C. and Gratto, C.J. 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. *Journal of Wildlife Management*. 59:93-98.

Creel, S., Creel, N.M., Monfort, S.L. 1997. Radiocollaring and stress hormones in African wild dogs. *Conservation Biology*. 11:544-548.

Cross, N. and Rogers, L.J. 2004. Diurnal cycle in salivary cortisol levels in common marmosets. *Developmental Psychobiology*. 45(3):134-139.

Curtis, D., Zaramody, A, Martin, RD. 1999. Cathemerality in the Mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology*. 47:279–298.

Cyr, N.E. and Michael Romero, L. 2007. Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *General and Comparative Endocrinology*. 151(1):82-89.

Czekala, N.M., Lance, V.A., Sutherland-Smith, M. 1984. Diurnal urinary corticoid excretion in the human and gorilla. *American Journal of Primatology*. 34:29-34.

da Silva Mota, M.T., Franci, C.R., de Sousa, M.B.C. 2006. Hormonal changes related to paternal and alloparental care in common marmosets *(Callithrix jacchus)*. *Hormones and Behavior*. 49:293-302.

Daan, S. and Tinbergen, J.M. 1997. Adaptation to Life Histories. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach, Fourth Edition*. Oxford: Blackwell Science. Pp. 311-333.

DaGosto, M. 1989. Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 78:209.

Dallman, M. 2003. Stress by any other name…? *Hormones and Behavior*. 43(1):18-20.

Dallman, M.F. 1993. Stress update: Adaptation of the hypothalamic-pituitary-adrenal axis to chronic stress. *Trends in Endocrinology and Metabolism*. 4(2):62-69.

Dallman, M.F., Strack, A.M., Akana, S.F., Bradbury, M.J., Hanson, E.S., Scribner, K.A., Smith, M. 1993. Feast and famine: Critical role of glucocorticoids with insulin in daily energy-flow. *Frontiers in Neuroendocrinology*. 14(4):303-347.

de Pedro, N., Delgado, M.J., Pinillos, M.L., Alonso-Gomez, A.L., Alonso-Bedate, M. 1998. Daily rhythms in NAT activity, cortisol, glucose, glycogen and catecholamines in tench (*Tinca tinca*). *Polskie Archiwum Hydrobiologii* 45(3):321-329.

Dettmer, E.L., Phillips, K.A., Rager, D.R., Bernstein, I.S., Fragaszy, D.M. 1996. Behavioral and cortisol responses to repeated capture and venipuncture in *Cebus apella*. *American Journal of Primatology*. 38(4):357-362.

Dewar, R.E. and Richard, A.F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences*. 104(34):13723-13727.

Di Bitetti, M.S. and Janson, C.H. 2000. When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*. 50:109-130.

Dobbin, J.P., Marth, M., McCain, G.A., Martin, R.A., Cousin, K. 1991. Cytokine production and lymphocyte transformation during stress. *Brain Behavior and Immunity*. 5:339-348.

Drent, R.H. and Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea*. 68(1-4):225-252.

DuPuy, D.J., Moat, J. 1995. A refined classification of the primary vegetation based on the underlying geology: Using GIS to map its distribution and to assess its conservation status. In: W.R. Laurenco, editor. *Biogeography of Madagascar*. Paris: Unesco. Pp. 205-218.

Engqvist, A. and Richard, A.F. 1991. Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatologica*. 57:169-172.

Esch, G.W., Gibbons, J.W., Bourque, J.E. 1975. An analysis of the relationship between stress and parasitism. *American Midland Naturalist*. 93(2):339-353.

Estrada, A., Juan-Solano, S., Ortíz Martínez, T., Coates-Estrada, R. 1999. Feeding and general activity patterns of a howler monkey *(Alouatta palliata)* troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology*. 48(3):167-183.

Fernandez-Duque, E., Erkert, H.G. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinean Chaco. *Folia Primatologica*. 77:123–138.

Fichtel, C., Kraus, C., Ganswindt, A., Heistermann, M. 2007. Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas *(Propithecus verreauxi)*. *Hormones and Behavior.* 51(5):640-648.

Fivizzani, A.J., Spieler, R.E., Noeske, T.A. 1984. The influence of ambient temperature on the daily variation of serum cortisol in the Banded Killifish, *Fundulus diaphanus*. *Journal of Interdisciplinary Cycle Research*. 15(1):3-8.

Fleming, A.S., Corter, C., Stallings, J., Steiner, M. 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*. 42:399-413.

Foley, C.A.H., Papageorge, S., Wasser, S.K. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*. 15(4):1134-1142.

French, J.A., Koban, T., Rukstalis, M., Ramirez, S.M., Bardi, M., Brent, L. 2004. Excretion of urinary steroids in pre- and postpartum female baboons. *General and Comparative Endocrinology*. 137(1):69-77.

Fulkerson, W.J. and Tang, B.Y. 1979. Ultradian and circadian rhythms in the plasma concentration of cortisol in sheep. *Journal of Endocrinology*. 81(1):135-141.

Ganzhorn, J.U. 1995a. Cyclones over Madagascar: Fate or fortune? *Ambio*. 24:124-125.

Ganzhorn, J.U., Langrand, O., Wright, P.C., O'Connor, S., Rakotosamimanana, B., Feistner, A.T.C., Rumpler, Y. 1996/7. The state of lemur conservation in Madagascar. *Primate Conservation*. 17:70-86.

Ganzhorn, J.U., Malcomber, S., Andrianantoanina, O., Goodman, S.M. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica*. 29(3):331-343.

Ganzhorn, J.U., Fietz, J., Rakotovao, E., Schwab, D., Zinner, D. 1999a. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*. 13:794-804.

Ganzhorn, J., Wright, P., Ratsimbazafy, H. 1999b. Primate communities: Madagascar. In: J.G. Fleagle, C.H. Janson and K. Reed, editors. *Primate Communities*. Cambridge: Cambridge University Press. Pp. 75-89.

Glander, K.E., Wright, P.C., Daniels, P.S., Merenlender, A.M. 1992. Morphometrics and testicle size in rain forest lemur species from southwestern Madagascar. *Journal of Human Evolution*. 92:1-17.

Glessner, K.D.G. and Britt, A. 2005. Population density and home range size of *Indri indri* in a protected low altitude rain forest. *International Journal of Primatology*. 26(4):855-872.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*. 123:250-276.

Gould, L., Ziegler, T.E., Wittwer, D.J. 2005. Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs *(Lemur catta)* at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*. 67(1):5-23.

Goymann, W., Möstl, E., Van't Hof, T., East, M.L., Hofer, H. 1999. Noninvasive fecal monitoring of glucocorticoids in spotted hyenas, *Crocuta crocuta*. *General and Comparative Endocrinology*. 114(3):340-348.

Goymann, W., East, M.L., Wachter, B., Honer, O.P., Möstl, E., Van't Hof, T.J., Hofer, H. 2001. Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 268(1484):2453-2459.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Green, G.M. and Sussman, R.W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*. 248:212-215.

Gross, T. 1991. Development and use of fecal steroid analyses in captive exotic mammals and birds. *Society for Theriogenology, Proceedings of Annual Meeting*: Pp. 66-74.

Gust, D.A., Gordon, T.P., Hambright, M.K. 1993. Response to removal from and return to a social group in adult male rhesus monkeys. *Physiology & Behavior*. 53(3):599-602.

Gust, D.A., Gordon, T.P., Wilson, M.E., Brodie, A.R., Ahmed-Ansari, A., McClure, H.M. 1996. Group formation of female pigtail macaques *(Macaca nemestrina)*. *American Journal of Primatology*. 39:263-273.

Gust, D.A., Wilson, M.E., Stocker, T., Conrad, S., Plotsky, P.M., Gordon, T.P. 2000. Activity of the hypothalamic-pituitary-adrenal axis is altered by aging and exposure to social stress in female rhesus monkeys. *Journal of Clinical Endocrinology and Metabolism*. 85(7):2556-2563.

Hammond, K.A. and Diamond, J. 1997. Maximal sustained energy budgets in humans and animals. *Nature*. 386:457-462.

Harcourt, C. and Thornback, J. 1990. *Lemurs of Madagascar and the Comoros. The IUCN Red Data Book*. Gland, Switzerland: IUCN.

Harlow, H.J., Thorne, E.T., Williams, E.S., Belden, E.L., Gern, W.A. 1987. Cardiac frequency: A potential predictor of blood cortisol levels during acute and chronic stress exposure in Rocky Mountain bighorn sheep *(Ovis canadensis)*. *Canadian Journal of Zoology*. 65:2028-2034.

Harper, J.N. and Austad, S.M. 2002. Fecal glucocorticoids: a noninvasive method of measuring adrenal activity in wild and captive rodents. *Physiological and Biochemical Zoology*. 73:12-22.

Hay, M. and Mormede, P. 1998. Urinary excretion of catecholamines, cortisol and their metabolites in Meishan and Large White sows: validation as a non-invasive and integrative assessment of adrenocortical and sympathoadrenal axis activity. *Veterinary Research*. 29(2):119-128.

Hemingway, C.A. 1995. *Feeding and Reproductive Strategies of* Propithecus diadema edwardsi [Doctoral Dissertation]. Durham: Duke University.

Hemingway, C.A. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edward's sifaka, *Propithecus diadema edwardsi,* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 17:637-657.

Hemingway, C.A. and Overdorff, D.J. 1999b. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. *Biotropica*. 31:354-364.

Hennessy, M.B., Mendoza, S.P., Mason, W.A., Moberg, G.P. 1995. Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*. 57(2):331-338.

Hennessy, M.B., Heybach, J.P., Vernikos, J., Levine, S. 1979. Plasma corticosterone concentrations sensitively reflect levels of stimulus intensity in the rat. *Physiology and Behavior*. 22:821-825.

Hofer, H. and East, M.L. 1998. Biological conservation and stress. In: A.P. Møller, M. Milinski and P.J.B. Slate, editors. *Advances in the Study of Behavior, Vol. 27*. San Diego: Academic Press. Pp. 405-525.

Homan, R.N., Regosin, J.V., Rodrigues, D.M., Reed, J.M., Windmiller, B.S., Romero, L.M. 2003. Impacts of varying habitat quality on the physiological stress of spotted salamanders *(Ambystoma maculatum)*. *Animal Conservation*. 6(1):11-18.

Honess, P.E. and Marin, C.M. 2006. Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews*. 30(3):390-412.

Hruschka, D.J., Kohrt, B.A., Worthman, C.M. 2005. Estimating between- and within-individual variation in cortisol levels using multilevel models. *Psychoneuroendocrinology*. 30(7):698-714.

Huber, S., Palme, R., Arnold, W. 2003. Effects of season, sex, and sample collection on concentrations of fecal cortisol metabolites in red deer *(Cervus elaphus)*. *General and Comparative Endocrinology*. 130(1):48-54.

Humphries, M.M., Umbanhowar, J., McCann, K.S. 2004. Bioenergetic prediction of climate change impacts on northern mammals 1. *Integrative and Comparative Biology*. 44(2):152-162.

Irwin, M.T. 2006. *Ecological Impacts of Forest Fragmentation on Diademed Sifakas* (Propithecus diadema) *at Tsinjoarivo, eastern Madagascar: Implications for Conservation in Fragmented Landscapes* [Doctoral Dissertation]. Stony Brook, New York: Stony Brook University. 410 p.

Irwin, M.T., Johnson, S.E., Wright, P.C. 2005. The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx*. 39(2):204-218.

Johnson, B.K. 2002. *Soil characterization and reconnaissance survey of the Ranomafana National Park area, southeastern Madagascar* [Doctoral Dissertation]. Raleigh, NC: North Carolina State University.

Johnson, S.E. and Overdorff, D.J. 1999. Census of brown lemurs (*Eulemur fulvus* spp.) in southeastern Madagascar: Methods-testing and conservation implications. *American Journal of Primatology*. 47(1):51-60.

Jolly, A. 1966. *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.

Jolly, A. 1984. The puzzle of female feeding priority. In: M. Small, editor. *Female Primates: Studies by Women Primatologists*. New York: Alan R. Liss. Pp. 197-215.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*. 78(1):57-66.

Kaplan, J.R. 1986. Psychological stress and behavior in nonhuman primates. In: G. Mitchell and J. Erwin, editors. *Comparative Primate Biology*. New York: Alan R. Liss.

Kappeler, P.M. 1996. Causes and consequences of life-history variation among strepsirhine primates. *American Naturalist*. 148:868-891.

Keay, J.M., Singh, J., Gaunt, M.C., Kaur, T. 2006. Fecal glucocorticoids and their metabolites as indicators of stress in various mammalian species: A literature review. *Journal of Zoo and Wildlife Medicine*. 37(3):234-244.

Keller, S.E., Weiss, J.M., Schleifer, S.L., Miller, N.E., Stern, M. 1983. Stress-induced suppression of immunity in adrenalectomized rats. *Science*. 221:1301-1304.

Khansari, D.N., Murgo, A.J., Faith, R.E. 1990. Effects of stress on the immune system. *Immunology Today*. 11:170-175.

Knott, C.D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*. 19:1061-1079.

Kraus, C., Heistermann, M., Kappeler, P.M. 1999. Physiological suppression of sexual function of subordinate males. A subtle form of intrasexual competition among male sifakas *(Propithecus verreauxi)*? *Physiology and Behavior*. 66:855-861.

Kurland J.A., and Pearson J.D. 1986. Ecological significance of hypometabolism in nonhuman primates: Allometry, adaptation, and deviant diets. *American Journal of Physical Anthropology*. 71*:*445–457.

Kuznetsov, V.A., Tchabovsky, A.V., Kolosova, I.E., Moshkin, M.P. 2004. Effect of habitat type and population density on the stress level of Midday Gerbils (*Meriones meridianus* Pall.) in free-living populations. *Biology Bulletin*. 31(6):628-632.

Lack, D. 1950. The breeding seasons of European birds. *Ibis*. 92:288-316.

Lancaster, J.B. and Lee, R.B. 1965. The annual reproductive cycle in monkeys and apes. In: I. DeVore, editor. *Primate Behavior: Field Studies of Monkeys and Apes*. New York: Holt, Rinehart and Winston.

Lane, J. 2006. Can non-invasive glucocorticoid measures be used as reliable indicators of stress in animals? *Animal Welfare*. 15(4):331-342.

Laudenslager, M.L., Ryan, S.M., Drugan, R.C., Hyson, R.L., Maier, S.F. 1983. Coping and immunosuppression: Inescapable but not escapable shock suppresses lymphocyte proliferation. *Science*. 221:568-570.

Lee, A.K. and Cockburn, A. 1985. *Evolutionary Ecology of Marsupials*. Cambridge: Cambridge University Press.

Lichtenbelt, W.D.V. 1993. Optimal foraging of a herbivorous lizard, the Green Iguana in a seasonal environment. *Oecologia*. 95(2):246-256.

Lindner, H.R. 1972. Enterohepatic circulation and patterns of urinary excretion of cortisol metabolites in the ewe. *Journal of Endocrinology*. 52:19-20.

Lucas, J.R., Freeberg, T.M., Egbert, J., Schwabl, H. 2006. Fecal corticosterone, body mass, and caching rates of Carolina chickadees *(Poecile carolinensis)* from disturbed and undisturbed sites. *Hormones and Behavior*:634-643.

Lynch, J.W., Ziegler, T.E., Strier, K.B. 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male Tufted Capuchin monkeys, *Cebus apella nigritus*. *Hormones and Behavior*. 41:275-287.

MacPhee, R.D.E. and Burney, D.A. 1991. Dating of modified femora of extinct dwarf hippopotamus from southern Madagascar: Implications for constraining human colonialism and vertebrate extinction events. *Journal of Archaeological Science*. 18:695-706.

Martínez-Mota, R., Valdespino, C., Sánchez-Ramos, M.A., Serio-Silva, J.C. 2007. Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Animal Conservation*. 10:374-379.

Mashburn, K.L. and Atkinson, S. 2004. Evaluation of adrenal function in serum and feces of Steller sea lions *(Eumetopias jubatus)*: influences of molt, gender, sample storage, and age on glucocorticoid metabolism. *General and Comparative Endocrinology*. 136(3):371-381.

Mateo, J.M. and Cavigelli, S.A. 2005. A validation of extraction methods for noninvasive sampling of glucocorticoids in free-living ground squirrels. *Physiological and Biochemical Zoology*. 78(6):1069-1084.

May, R.M. and Rubenstein, D.I. 1985. Reproductive strategies. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals: Reproductive Fitness, Book 4*. New York: Cambridge University Press. Pp. 1-23.

McCallister, J.M., Smith, T.E., Elwood, R.W. 2004. Validation of urinary cortisol as an indicator of hypothalamic-pituitary-adrenal function in the bearded emperor tamarin (*Saguinus imperator subgrisescens*). *American Journal of Primatology*. 63(1):17-23.

McEwen, B.S. and Wingfield, J.C. 2003a. The concept of allostasis in biology and biomedicine. *Hormones and Behavior*. 43(1):2-15.

McEwen, B.S. and Wingfield, J.C. 2003b. Response to commentaries on the concept of allostasis. *Hormones and Behavior*. 43(1):28-30.

McKenzie, S. and Deane, E.M. 2005. Faecal corticosteroid levels as an indicator of well-being in the tammar wallaby, *Macropus eugenii*. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology*. 140(1):81-87.

Mendoza, S.P. and Mason, W.A. 1988. Behavioral and endocrine consequences of heterosexual pair formation in squirrel monkeys. *Physiology and Behavior*. 46:597-603.

Merenlender, A., Kremen, C., Rakotondratsima, M., Weiss, A. 1998. Monitoring impacts of natural resource extraction on lemurs of the Masoala Peninsula, Madagascar. *Conservation Ecology* 2(2):5-29.

Miller, M.W., Hobbs, N.T., Sousa, M.C. 1991. Detecting stress responses in Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*): Reliability of cortisol concentrations in urine and feces. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 69(1):15-24.

Millspaugh, J.J. and Washburn, B.E. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *General and Comparative Endocrinology*. 138(3):189-199.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersalll, I., Meyers, D.M. 2006. *Lemurs of Madagascar. 2nd Edition*. Washington, DC: Conservation International.

Monfort, S.L., Wasser, S.K., Mashburn, K.L., Burke, M., Brewer, B.A., Creel, S.R. 1997. Steroid metabolism and validation of noninvasive endocrine monitoring in the African wild dog *(Lycaon pictus)*. *Zoo Biology*. 16(6):533-548.

Moore, I.T. and Jessop, T.S. 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Hormones and Behavior*. 43(1):39-47.

Morland, H.S. 1991. Preliminary report on the social organization of ruffed lemurs *(Varecia variegata variegata)* in a northeast Madagascar rainforest. *Folia Primatologica*. 56:157-161.

Morland, H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 193-203.

Möstl, E., Maggs, J.L., Schrotter, G., Besenfelder, U., Palme, R. 2002. Measurement of cortisol metabolites in faeces of ruminants. *Veterinary Research Communications*. 26(2):127-139.

Möstl, E. and Palme, R. 2002. Hormones as indicators of stress. *Domestic Animal Endocrinology*. 23:67-74.

Muehlenbein, M.P. 2006. Intestinal parasite infections and fecal steroid levels in wild chimpanzees. *American Journal of Physical Anthropology*. 130:546-550.

Müller, M.N. and Wrangham, R. 2004. Dominance, cortisol and stress in wild chimpanzees *(Pan troglodytes schweinfurthii)*. *Behavioral Ecology and Sociobiology*. 55:332-340.

Mutschler, T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur *(Hapalemur griseus alaotrensis)*. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Press. Pp. 221–239.

Nash, L.T. 1998. Vertical clingers and sleepers 1: Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*. 69(Suppl. 1):204-217.

Nash, L.T. 1999. Factors influencing census results on *Lepilemur* and *Microcebus* in southwestern Madagascar. *American Journal of Physical Anthropology*. S28:209.

Negus, N.C. and Berger, P.J. 1972. Environmental factors and reproductive processes in mammalian populations. In: J.T. Velardo and B.A. Kasprow, editors. *Biology of Reproduction: Basic and Clinical Studies*; *Third Pan American Congress on Anatomy*, New Orleans. Pan American Association of Anatomy: Pp. 89-98.

Nelson, R. and Horning, N. 1993. AVHRR-LAC estimates of forest area in Madagascar, 1990. *International Journal of Remote Sensing*. 14:1463-1475.

Nelson, R.J. and Klein, S.L. 1999. Environmental and social influences on seasonal breeding and immune function. In: K. Wallen and J.E. Schneider, editors. *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior*. Cambridge: MIT Press Pp. 219-256.

Nelson, R.J., Demas, G.E., Klein, S.L., Kriegsfeld, L.J. 2002. *Seasonal Patterns of Stress, Immune Function, and Disease*. Cambridge University Press.

Nisbet, I.C.T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds*. 23:312–332.

Norris, D.O., Donahue, S., Dores, R.M., Lee, J.K., Maldonado, T.A., Ruth, T., Woodling, J.D. 1999. Impaired adrenocortical response to stress by brown trout, *Salmo trutta*, living in metal-contaminated waters of the Eagle River, Colorado. *General and Comparative Endocrinology*. 113(1):1-8.

Nunes, S., Fite, J.E., Patera, K.J., French, J.A. 2001. Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets *(Callithrix kuhli)*. *Hormones and Behavior*. 39:70-82.

Oates, J.F. 1977. The guereza and its food. In: T.H. Clutton-Brock, editor. *Primate Ecology*. London: Academic Press. Pp. 276-319.

Ostner, J., Kappeler, P.M., M., H. 2002. Seasonal variation and social correlates of androgen excretion in male redfronted lemurs *(Eulemur fulvus rufus)*. *Behavioral Ecology and Sociobiology*. 52:485-495.

Overdorff, D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D.J. 1991. *Ecological correlates to social structure in two prosimian primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral Dissertation]. Durham: Duke University. 313 p.

Overdorff, D.J. 1993a. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. *International Journal of Primatology*. 14(5):721-753.

Overdorff, D.J. 1993b. Ecological and reproductive correlates with ranging patterns in two prosimian primates in Madagascar. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 167-192.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40(4):327-342.

Overdorff, D.J. 1996b. Ecological correlates to social structure in two lemur species in Madagascar. *American Journal of Physical Anthropology*. 100(4):487-506.

Overdorff, D.J. and Rasmussen, M.A. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 61-74.

Overdorff, D.J. and Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Overdorff, D.J. and Tecot, S. R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 235-245.

Overdorff, D.J., Merenlender, A.M., Talata, P., Telo, A., Forward, Z.A. 1999. Life history of *Eulemur fulvus rufus* from 1988-1998 in southeastern Madagascar. *American Journal of Physical Anthropology*. 108:295-310.

Palme, R., Robia, C., Messmann, S., Hofer, J., Möstl, E. 1999. Measurement of faecal cortisol metabolites in ruminants: a non-invasive parameter of adrenocortical function. *Wiener Tierarztliche Monatsschrift*. 86(7):237-241.

Paterson, A.M. and Pearce, G.P. 1992. Growth response to humans and corticosteroids in male pigs housed individually and subjected to pleasant, unpleasant or minimal handling during rearing. *Applied Animal Behavior Science*. 34:315-328.

Peel, A.J., Vogelnest, L., Finnigan, M., Grossfeldt, L., O'Brien, J.K. 2005. Non-invasive fecal hormone analysis and behavioral observations for monitoring stress responses in captive western lowland gorillas *(Gorilla gorilla gorilla)*. *Zoo Biology*. 24(5):431-445.

Pereira, M. 1993. Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 205-221.

Pereira, M.E., Russ, A.S., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Publishers.

Perret, M. and Predine, J. 1984. Effects of long-term grouping on serum cortisol levels in *Microcebus murinus* Prosimii. *Hormones and Behavior*. 18(3):346-358.

Pochron, S.T., Tucker, W.T., Wright, P.C. 2004. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 125:61-72.

Pollack, J.I. 1979. Spatial distribution and ranging behavior in lemurs. In: G.A. Doyle and R.D. Martin, editors. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 359–409.

Porter, L.M. 1998. Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. *Folia Primatologica*. 69(3):172-176.

Powzyk, J.A. 1997. *The Socio-ecology of Two Sympatric Indriids:* Propithecus diadema diadema *and* Indri indri*, a Comparison of Feeding Strategies and Their Possible Repercussions on Species-Specific Behaviors.* [Doctoral Dissertation]. Durham, NC: Duke University.

Pride, E. 2005a. Optimal group size and seasonal stress in ring-tailed lemurs *(Lemur catta)*. *Behavioral Ecology*. 16(3):550-560.

Pride, E. 2005b. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs *(Lemur catta)*. *Biological Letters*. 1:60-63.

Rasmussen, M.A. 1999. *Ecological Influences on Activity Cycle in Two Cathemeral Primates, the Mongoose Lemur* (Eulemur mongoz) *and the Common Brown*

Lemur (Eulemur fulvus fulvus) [Doctoral Dissertation]. Durham, North Carolina: Duke University.

Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B., Cunningham, E.J.A. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society B*. 273:2713-2719.

Reeder, D.M. and Kramer, K.M. 2005. Stress in free-ranging mammals: Integrating physiology, ecology, and natural history. *Journal of Mammalogy*. 86(2):225-235.

Rich, E.L. and Romero, L.M. 2005. Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*. 288(6):R1628-R1636.

Richard, A.F. and Dewar, R.E. 1991. Lemur ecology. *Annual Review of Ecology and Systematics* 22:145–175.

Richard, A.F. and Nicoll, M.E. 1987. Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology*. 12:309-314.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*. 39(4):381-391.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Risler, L., Wasser, S.K., Sackett, G.P. 1987. Measurement of excreted steroids in *Macaca nemestrina*. *American Journal of Primatology*. 12(1):91-100.

Rodway, M.S., Montevecchi, W.A., Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic puffins *(Fratercula arctica)*. *Biological Conservation*. 76:311-319.

Romero, M.L. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*. 128:1-24.

Romero, L.M. 2004. Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*. 19(5):249-255.

Romero, L.M. and Remage-Healey, L. 2000. Daily and seasonal variation in response to stress in captive starlings *(Sturnus vulgaris)*: Corticosterone. *General and Comparative Endocrinology*. 119(1):52-59.

Rose, R.M., Gordon, T., Bernstein, I.S. 1978. Diurnal variation in plasma testosterone and cortisol in rhesus monkeys living in social groups. *Journal of Endocrinology*. 76:67-74.

Rusak, B. 1989. The mammalian circadian system: Models and physiology. *Journal of Biological Rhythms*. 4(2):121-134.

Saboureau, M., Laurent, G., Boissin, J. 1979. Daily and seasonal rhythms of locomotor activity and adrenal function in male hedgehogs *(Erinaceus europaeus)*. *Journal of Interdisciplinary Cycle Research*. 10(4):249-266.

Saltzman, W., Schultz-Darken, N.J., Scheffler, G., Wegner, F.H., Abbott, D.H. 1994. Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*. 56(4):801-810.

Sapolsky, R.M. 1982. The endocrine stress response and social status in the wild baboon. *Hormones and Behavior*. 16:279–292.

Sapolsky, R.M. 1983. Endocrine aspects of social instability in the olive baboon *(Papio anubis)*. *American Journal of Primatology*. 5:365-379.

Sapolsky, R.M. 1985. Stress-induced suppression of testicular function in the wild baboon: Role of glucocorticoids. *Endocrinology*. 116:2273-2278.

Sapolsky, R.M. 1986. Endocrine and behavioral correlates of drought in the wild baboons. *American Journal of Primatology*. 11:217-226.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons. In: D. Crews, editor. *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*. Englewood Cliffs, New Jersey: Prentice Hall. Pp. 291-322.

Sapolsky, R.M. 1991. Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*. 16(4):281-293.

Sapolsky, R.M. 1992. *Stress, the Aging Brain, and the Mechanisms of Neuron Death*. Cambridge: MIT Press.

Sapolsky, R.M. 1994. *Why Zebras Don't Get Ulcers: A Guide to Stress, Stress-Related Diseases, and Coping*. New York: W.H. Freeman.

Sauerwein, H., Müller, U., Brüssel, H., Lutz, W., Möstl, E. 2004. Establishing baseline values of parameters potentially indicative of chronic stress in red deer *(Cervus elaphus)* from different habitats in western Germany. *European Journal of Wildlife Research*. 50:168–172.

Sauther, M.L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ringtailed lemur conservation. *Folia Primatologica*. 69:309-320.

Sauther, M.L. 1993. Resource competition in wild populations of ringtailed lemurs *(Lemur catta)*: Implications for female dominance. In: P. M. Kappeler and J. U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum. Pp. 135–152.

Sayre, R.W. 1996. *Ecology of Bighorn Sheep in Relation to Habitat and Oil* [Doctoral Dissertation]: University of North Dakota. 138 p.

Schapiro, S.J., Bloomsmith, M.A., Kessel, A.L., Shively, C.A. 1993. Effects of enrichment and housing on cortisol response in juvenile rhesus monkeys. *Applied Animal Behaviour Science*. 37(3):251-263.

Schiml, P.A., Mendoza, S.P., Saltzman, W., Lyons, D.M., Mason, W.A. 1996. Seasonality in squirrel monkeys *(Saimiri sciureus)*, social facilitation by females. *Physiology & Behavior*. 60(4):1105-1113.

Schmid, J. and Ganzhorn, J.U. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. *American Journal of Primatology*. 38:169-174.

Schoech, S.J., Bowman, R., Bridge, E.S., Boughton, R.K. 2007. Baseline and acute levels of corticosterone in Florida Scrub-Jays *(Aphelocoma coerulescens)*: Effects of food supplementation, suburban habitat, and year. *General and Comparative Endocrinology*. 154(1-3):150-160.

Schulkin, J. 2003. Allostasis: a neural behavioral perspective. *Hormones and Behavior*. 43(1):21-27.

Selye, H. 1950. *Stress*. Montreal: ACTA, Incorporated.

Selye, H. 1956. *The Stress of Life*. New York: McGraw-Hill.

Selye, H. 1980. *Selye's Guide to Stress Research, Vol.1*. New York: Van Nostrand Reinhold Company.

Smith, T.E. and French, J.A. 1997. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets *(Callithrix kuhli)*. *American Journal of Primatology*. 42:253-267.

Smith, A.P. and Ganzhorn, J.U. 1996. Convergence and divergence in community structure and dietary adaptations in Australian possums and gliders and Malagasy lemurs. *Australian Journal of Ecology*. 21:31-46.

Snodgrass, J.J., Leonard, W.R., Robertson, M.M.M. 2007. Primate bioenergetics: an evolutionary perspective. *Primate Origins: Adaptations and Evolution*. New York: Springer. Pp. 703-737.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. San Francisco: W.H. Freeman.

Sørg, J.-P. and Røhner, U. 1996. Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. *Primate Report*. 46(1):57-80.

Sousa, M.B.C. and Ziegler, T.E. 1998. Diurnal variation on the excretion patterns of fecal steroids in common marmoset *(Callithrix jacchus)* females. *American Journal of Primatology*. 46(2):105-117.

Stavisky, R.C., Wilson, M., Russell, E., Whitten, P.L. 1994. Validation of the fecal extraction method: Correlation of serum and fecal endocrine profiles in rhesus macaques, *Macaca mulatta*. *American Journal of Physical Anthropology*. (S18):186.

Stavisky, R.C., Whitten, P.L., Hammett, D.H., Kaplan, J.R. 2001a. Lake pigments facilitate analysis of fecal cortisol and behavior in group-housed macaques. *American Journal of Physical Anthropology*. 116(1):51-58.

Stavisky, R.C., Brandenberger, D., Hook, M., Russell, E., Kaplan, J., Whitten, P. 2001b. The effect of menstrual cycle phase on cortisol excretion on female cynomolgus monkeys *(Macaca fascicularis)*. *American Journal of Primatology*. 54(S1):39-40.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review in Biology*. 51:3-47.

Sterling, P. and Eyer, J. 1988. Allostasis: A new paradigm to explain arousal pathology. In: S. Fisher and J. Reason, editors. *Handbook of Life Stress, Cognition and Health*. New York: John Wiley & Sons.

Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E. 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution of Human Behavior*. 21:79-95.

Strier, K.B. and Ziegler, T.E. 1997. Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *American Journal of Primatology*. 42(4):299-310.

Strier, K.B. and Ziegler, T.E. 2005. Advances in field-based studies of primate behavioral endocrinology. *American Journal of Primatology*. 67(1):1-4.

Strier, K.B., Ziegler, T.E., Wittwer, D.J. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis *(Brachyteles arachnoides)*. *Hormones and Behavior*. 35:125-134.

Tarlow, E.M. and Blumstein, D.T. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*. 102(3-4):429-451.

Tattersalll, I. 1987. Cathemeral activity in primates - a definition. *Folia Primatologica*. 49(3-4):200-202.

Tecot, S. 1999. *The effect of habitat on fecal cortisol concentrations in squirrel monkeys* (Saimiri sciureus) [Master's Thesis]. Austin: University of Texas at Austin.

Tecot, S. 2001. Field methods for collecting fecal cortisol: A test of four Malagasy primates. *American Journal of Primatology*. 54(S1):32-33.

Tecot, S. 2006. Activity budget and microhabitat in *Eulemur rubriventer*. *American Journal of Primatology*. 68(1):111-112.

Tecot, S. 2007a. Seasonality, phenology, and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. S44:230.

Tecot, S. 2007b. Fecal cortisol levels and maintenance behaviors in wild groups of a cooperatively breeding species, the red-bellied lemur *(Eulemur rubriventer)*. *American Journal of Primatology*. 69(1):127.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Terborgh, J. 1986b. Keystone plant resources in the tropical forest. In: M.E. Soulé, editor. *Conservation Biology, the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc. Pp. 330–344.

Terio, K.A., Citino, S.B., Brown, J.L. 1999. Fecal cortisol metabolite analysis for noninvasive monitoring of adrenocortical function in the cheetah *(Acinonyx jubatus)*. *Journal of Zoo and Wildlife Medicine*. 30(4):484-491.

Terranova, C.J., Coffman, B.S. 1997. Body weights of wild and captive lemurs. *Zoo Biology*. 16(1):17-30.

Tilden, C.D. and Oftedal, O.T. 1995. The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: L Alterman, G.A. Doyle and M.K. Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 119-131.

Touma, C. and Palme, R. 2005. Measuring fecal glucocorticoid metabolites in mammals and birds: The importance of validation. *Annals of the New York Academy of Sciences*. 1046(1):54-74.

Touma, C., Palme, R., Sachser, N. 2004. Analyzing corticosterone metabolites in fecal samples of mice: a noninvasive technique to monitor stress hormones. *Hormones and Behavior*. 45(1):10-22.

Turk, D. 1995. *A Guide to the Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Ulyan, M.J., Burrows, A.E., Buzzell, C.A., Raghanti, M.A., Marcinkiewicz, J.L., Phillips, K.A. 2006. The effects of predictable and unpredictable feeding schedules on the behavior and physiology of captive brown capuchins *(Cebus apella)*. *Applied Animal Behaviour Science*. 101:154-160.

van Horn, R.N. and Eaton, G.G. 1979. Reproductive physiology and behavior in prosimians. In: R. D. Martin, editor. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 79-122.

van Schaik, C., and van Noordwijk, MA. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques *(Macaca fascicularis)*. *Journal of Zoology*. 206:533-549.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs *(Varecia rubra)* on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. *American Journal of Primatology*. 66(4):393-394.

von der Ohe, C.G., Wasser, S.K., Hunt, K.E., Servheen, C. 2004. Factors associated with fecal glucocorticoids in Alaskan Brown bears *(Ursus arctos horribilis)*. *Physiological and Biochemical Zoology*. 77(2):313-320.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2005. Field endocrinology and conservation biology. *Integrative and Comparative Biology*. 45:12-18.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2006. Habituation of adult magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology*. 20(1):146-154.

Walsberg, G.E. 2003. How useful is energy balance as a overall index of stress in animals? *Hormones and Behavior*. 43(1):16-17.

Wasser, S.K. and Starling, A.K. 1988. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology*. 16(2):97-121.

Wasser, S.K., Thomas, R., Nair, P.P., Guidry, C., Southers, J., Lucas, J., Wildt, D.E., Monfort, S.L. 1993. Effects of dietary fiber on faecal steroid measurements. *Journal of Reproduction and Fertility*. 97:569-574.

Wasser, S.K., Bevis, K., King, G., Hanson, E. 1997. Non-invasive physiological measures of disturbance in the Northern spotted owl. *Conservation Biology*. 11:1019–1022.

Wasser, S.K., Hunt, K.E., Brown, J.L., Cooper, K., Crockett, C.M., Bechert, U., Millspaugh, J.J., Larson, S., Monfort, S.L. 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *General and Comparative Endocrinology*. 120(3):260-275.

Watson, S.L., Ward, J.P., Davis, K.B., Stavisky, R.C. 1999. Scent-marking and cortisol response in the small-eared bushbaby *(Otolemur garnettii)*. *Physiology and Behavior*. 66(4):695-699.

Watts, D.P. 1988. Environmental influences on Mountain gorilla time budgets. *American Journal of Primatology*. 15:195-211.

Wehr, A. 1998. Effect of seasonal changes in daylength on human neuroendocrine function. *Hormone Research*. 49(3-4):118-124.

Weingrill, T., Gray, D.A., Barrett, L., Henzi, S.P. 2004. Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*. 45(4):259-269.

White, F., Overdorff, D.J., Balko, E., Wright, P.C. 1995. Distribution of ruffed lemurs *(Varecia variegata)* in Ranomafana National Park, Madagascar. *Folia Primatologica*. 64:124-131.

Whitten, P. 2000. Evolutionary endocrinology of the cercopithecoids. In: P.F. Whitehead and C.J. Jolly, editors. *Old World Monkeys*. Cambridge: Cambridge University Press. Pp. 269-297.

Whitten, P.L. and Brockman, D.K. 2001. Strepsirrhine reproductive ecology. In: P.T. Ellison, editor. *Reproductive Ecology and Human Evolution*. New York: Aldine de Gruyter. Pp. 321-350.

Whitten, P.L., Brockman, D.K., Stavisky, R.C. 1998a. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*. Pp. 1-23.

Whitten, P.L., Stavisky, R., Aureli, F., Russell, E. 1998b. Response of fecal cortisol to stress in captive chimpanzees *(Pan troglodytes)*. *American Journal of Primatology*. 44(1):57-69.

Wiebe, R.H., Williams, L.E., Abee, C.R., Yeoman, R.R., Diamond, E.J. 1988. Seasonal changes in serum dehydroepiandrosterone, androstenedione, and testosterone levels in the squirrel monkey (*Saimiri boliviensis boliviensis*). *American Journal of Primatology*. 14(3):285-291.

Wilson, M.I., Brown, G.M., Wilson, D. 1978. Annual and diurnal changes in plasma androgen and cortisol in adult male squirrel monkeys *(Saimiri sciureus)* studied longitudinally. *Acta Endocrinologica*. 87(2):424-433.

Wingfield, J.C. 2003. Anniversary Essay: Control of behavioural strategies for capricious environments. *Animal Behaviour*. 66:807-816.

Wingfield, J.C. and Kitaysky, A.S. 2002. Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? *Integrative and Comparative Biology*. 42:600-609.

Wingfield, J.C. and Romero, L.M. 2001. Adrenocortical responses to stress and their modulation in free-living vertebrates. In: B.S. McEwen and H.M. Goodman, editors. *Handbook of Physiology, Section 7: The Endocrine System, Vol. IV: Coping with the Environment: Neural and Endocrine Mechanisms*. New York: Oxford University Press. Pp. 211-234.

Wingfield, J.C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G.S., Freed, L., Lepson, J. 1997. Environmental stress, field endocrinology, and conservation biology. In: J.R. Clemmons and R. Buchholz, editors. *Behavioral Approaches to Conservation in the Wild* Cambridge: Cambridge University Press. Pp. 95-131.

Wright, P.C. 1992. Primate ecology, rainforest conservation and economic development: Building a national park in Madagascar. *Evolutionary Anthropology*. 1:25-33.

Wright, P.C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 16(5):835-854.

Wright, P.C. 1997. The future of biodiversity in Madagascar: A view from Ranomafana National Park. In: S. G. Goodman and B. D. Patterson, editor. *Natural Change and Human Impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press. Pp. 381-405.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*. 42:31-72.

Wright, P.C. 2006. Considering climate change effects in lemur ecology and conservation. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 385-401.

Wright, P.C. and Razafindratsita, T., Pochron, S.T., Jernvall, J. 2005. The key to frugivory in Madagascar. In: J.L. Dew and J.P. Boubli, editors. *Tropical Fruits and Frugivores: The Search for Strong Interactors.* New York: Kluwer Academic/Plenum. Pp. 118-128.

Young, A.L., Richard, A.F., Aiello, L.C. 1990. Female dominance and maternal investment in Strepsirhine primates. *American Naturalist*. 135:473-488.

Zav'yalov, E.L., Gerlinskaya, L.A., Evsikov, V.L. 2003. Estimation of stress level in the bank vole *Clethrionomys glareolus* (Rodentidae, Rodentia) by fecal corticosterone. *Zoologichesky Zhurnal*. 82(4):508-513.

Ziegler, T.E. 2000. Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*. 71:6-21.

Ziegler, T.E. and Tecot, S. 2007. Cooperative breeding in nonhuman primates: A broader approach. *American Journal of Primatology*. 69(1):126.

Ziegler, T.E. and Wittwer, D.J. 2005. Fecal steroid research in the field and laboratory: Improved methods for storage, transport, processing, and analysis. *American Journal of Primatology*. 67(1):159-174.

Ziegler, T.E., Scheffler, G., Snowdon, C.T. 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*. 29:407-424.

Ziegler, T.E., Wegner, F.H., Snowdon, C.T. 1996. Hormonal responses to parental and nonparental conditions in male cotton-top tamarins, *Saguinus oedipus*, a New World primate. *Hormones and Behavior*. 30(3):287-297.

Ziegler, T.E., Washabaugh, K.F., Snowdon, C.T. 2004. Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*. 45(2):84-92.

Chapter 5: Seasonality of Habitat, Behavior, and Fecal Cortisol Levels in *Eulemur rubriventer*: Conclusions and Implications for the Evolution of Lemurid Energetic Strategies

INTRODUCTION

In this final chapter information from the preceding chapters is synthesized to characterize energetic strategies in *Eulemur rubriventer* and postulate about energetic strategies used by lemurs in general. First, the seasonal environment was quantified and habitats were compared to establish differences between study sites and facilitate investigation of the effects of habitat disturbance. Second, time budgets were constructed to identify behavioral strategies of energy conservation and resource maximization, and determine how these strategies respond to the dynamic physical environment. Sites were viewed in tandem to elucidate how modifying factors differentially affect populations. Third, profiles of cortisol excretion were constructed and mapped onto changes observed in the physical environment to determine what parameters yield a physiological response in *Eulemur rubriventer*. These profiles were then viewed in relation to behavioral strategies to identify periods of energy storage and extraction and identify periods and criteria critical for successful reproduction. Inter-site comparisons were made to determine how habitats influence the possibilities for energy storage and extraction, and elucidate the relationship between habitat disturbance and cortisol excretion. Finally, these results are discussed below as they relate to models of lemurid evolution, and their implications for using this technique as a conservation monitoring tool.

THE SEASONAL ENVIRONMENT AND HABITAT DISTURBANCE

Madagascar's environment is notoriously harsh and unpredictable and has been invoked as an important factor shaping the evolution of unique lemurid traits (*e.g.,* Wright, 1999; Dewar and Richard, 2007). Rainfall in particular is notably variable from year to year (Dewar and Richard, 2007), and may explain inter-annual unpredictability of food resources. Precipitation is often regarded as the most influential factor in the timing of plant phenophase (Sørg and Røhner, 1996; Morellato *et al.* 2000), and positive relationships between rainfall and fruiting have been found in Madagascar (Atsalis, 1999a; Hemingway, 1996; Sørg and Røhner, 1996; Tecot, Chapter 2). Results from this study support the premise that inter-annual variation in rainfall is manifest in fruit availability.

Although rainfall has an important role, there was a great deal of variation between sites in the strength of the relationship between climate and phenological stage, supporting the assertion that climate is not always related to phenology in Ranomafana (Wright, 1999; Overdorff and Wright, unpublished manuscript), and that other factors such as soil and canopy cover probably play significant roles (Sørg and Røhner, 1996; Grassi, 2001; B. Johnson, 2002; Bollen and Donati, 2005). Such incongruent relationships across sites appear to result from habitat disturbance, which may alter the face of phenological scheduling in plants. Significant correlations between fruiting and both rainfall and minimum temperature were found in Vatoharanana (as reported for Ranomafana by Atsalis, 1999a), the undisturbed forest, but no significant correlations existed in Talatakely, the disturbed forest, located only a few kilometers away. The predictability of plant phenology in disturbed habitats may then not be determined by the

predictability of the climate, and rainfall and temperature may be less reliable indicators/cues for *Eulemur rubriventer* food availability at this disturbed site. Lower fruit, flower, and leaf productivity, lower species richness and diversity, and largely random fruiting in Talatakely may exacerbate the impact of the disjointed relationship between climate and phenology, indicating that the mechanism by which primate populations are threatened may be the unpredictable relationships between climate and phenology generated by habitat disturbance. These results also have important implications for large-scale models of the climate-phenological relationship in Madagascar and elsewhere. As pristine forests become rare around the world, knowledge of a forest's anthropogenic history becomes essential for a complete understanding of apparent patterns. Analyses of long-term databases of climate and phenology will be better equipped to assess the complex relationship between fruit and rainfall, and such studies would benefit from comparisons with other sites where species inventories, and therefore reproductive scheduling, vary.

These results are of critical importance: the availability of ripe fruit is exceptionally unpredictable in the disturbed forest, and this has great implications for population viability and life histories in these groups. Dewar and Richard (2007) suggested that high fruiting variance observed in Madagascar's flora resulted in the high reproductive variance observed in lemur species (Richard *et al.,* 2002; Gould *et al.,* 2003), including *Eulemur rubriventer* (Tecot and Overdorff, 2005). Lemurs appear to rely upon predictive cues about when food will be abundant, which facilitates timing weaning with food abundance (van Schaik and van Noordwijk, 1985; Wright, 1999). In support of this assertion, results from this study suggest that infant survivorship was

higher when late lactation/early weaning coincided with fruit abundance, and was not dependent upon the presence of fruit at birth. Furthermore, all infant mortality was localized to Talatakely. As a result, habitat disturbance has a clear effect upon reproductive success.

How do *Eulemur rubriventer* reproductive strategies compare with other lemurs? In general lemurs adopt an obligate (Negus and Berger, 1972) or income (Brockman and van Schaik, 2005) breeding strategy, relying upon what energy is currently present in the environment, cued by photoperiod. Living in environments without predictable cues as to when food will be available, however, requires extreme flexibility for primary consumers to survive and reproduce (Silver and Marsh, 2003). In fact, lemurs may also store energy (Pereira *et al.,* 1999), indicating that lemur breeding may be relaxed, and not strictly bound to photoperiodic cues. Such 'relaxed income' breeders (Brockman and van Schaik, 2005; also 'income II', Janson and Verdolin, 2005) are seasonal and rely upon predictive cues, timing late-lactation and weaning with food abundance, yet the ability to conceive depends upon the female's energetic condition. This study suggests that *Eulemur rubriventer* may be a relaxed income breeder, and that this effect upon reproduction may be intensified by additional unpredictability imparted by habitat disturbance, with even higher reproductive variance in disturbed habitats (as observed in this study). Without *reliable* predictive cues (such as photoperiod or climate) about when food will be available, infant survival for income breeders may become largely reliant upon the ability to store energy. This is the paradox of surviving and reproducing in disturbed habitats: unreliable cues necessitate maximizing resources for successful

breeding. Yet, resource availability is often reduced, prohibiting energy storage. Further study is necessary to determine whether

TIME BUDGETS: ENERGY CONSERVATION AND RESOURCE MAXIMIZATION STRATEGIES

Overall, *Eulemur rubriventer* were energetically conservative and adopted an energy/time minimizing strategy, resting approximately 75% of the time, similar to folivorous species though they feed upon fruit approximately 75% of the time. Although *E. rubriventer* are cathemeral and nighttime activity may change this result, Overdorff (1988) did not find any difference between daytime and nighttime activity. During the lean season an energy maximizing strategy was employed whereby lemurs rested less and fed more. *E. rubriventer* also employed energy maximizing strategies during weaning and parturition (feeding a high to moderate amount), the most energetically expensive times for females (Jolly, 1984; Coelho, 1986; Bronson and Heideman, 1994). In contrast with parturition, energy maximization during and just after weaning was coincident with fruit abundance and may indicate either relatively high energy requirements, or conversely, energy storage (see below), since energy maximization at other times occurred with fruit scarcity.

During gestation (May – September), a relatively less expensive reproductive stage, *E. rubriventer* employed a time/energy minimizing strategy. Energy minimizing strategies between the austral winter solstice and fall equinox have also been observed in *Varecia variegata* (Morland, 1993), and coincide with reduced juvenile and hair growth and decreased appetite in captive lemurs (Pereira *et al.,* 1993), and reductions in temperature in Madagascar. Pereira and colleagues (1993) further report that this is a

period of energy extraction from adipose tissue. As this period is not equivalent to gestation for all lemurs, this suite of responses—conservation of energy expenditure and extraction of energy from stores—may be best interpreted as a response to cooler temperatures and declining food, rather than a reproductive strategy *per se.*

In fact, several mammal species in Madagascar, including lemurs (*Microcebus* and *Cheirogaleus* (lemurs): Petter-Rousseaux, 1980, Wright & Martin, 1995, Schmid & Kappeler, 1998, Sørg *et al.*, 2003, Dausmann *et al.*, 2004; *Limnogale* (tenrecs): Nicoll, 2003, Stephenson, 2003; *Miniopterus* (bats): Eger and Mitchell, 2003; *Zonosaurus* (lizards): Raselimanana, 2003), enter hibernation or daily or extended torpor during winter. Species become inactive and body temperature and metabolic rates decrease (Lyman *et al.*, 1982; Wang, 1989). Hibernation is generally understood to be an adaptation to enable energy conservation in harsh environments (*e.g.,* Schmid & Stephenson, 2003). Prior to denning, hibernating species often increase activity (foraging and feeding) to accumulate fat reserves to use as energy during the period of inactivity. Viewed within this context, the behavioral strategies of *Eulemur rubriventer* such as increased activity prior to winter, and decreased activity during winter*,* support the suggestion that energy maximizing adjustments made prior to winter may enable such energetically conservative behavior during winter (Pereira *et al.,* 1999). An interesting question for further study might be whether basal metabolic rates in diurnal or cathemeral lemur species change seasonally, or even within one day during long bouts of rest. The results of this study suggest that *E. rubriventer* is able to fine-tune its energetic expenditure and intake to accommodate the very particular environmental circumstances it encounters at any given time. Habitat comparisons underscore this flexibility and

clarify the energetic circumstances under which the boundaries of this flexibility are met, and the point at which this delicate balance may be upset and put primary consumers at greater risk.

Time Budgets and Habitat Disturbance: Site Comparisons

Viewing energetic strategies in each site relative to the other highlighted limitations to energy accumulation in Talatakely, the disturbed site. Relative to each other, *E. rubriventer* in Talatakely conserved energy while those in Vatoharanana maximized energy. When an environment is degraded and resources are scarce, more time spent resting relative to groups in more pristine habitat may be the only available option to maintain enough energy for survival and reproduction (*cf* Nash, 1998). Moreover, a time budget which maximizes energy relative to another time budget (which necessarily minimizes energy expenditure) may indicate energy storage versus merely filling current energy requirements (Hemingway, 1999; see Atsalis, 1999b and Lewis and Kappeler, 2005 for studies of fat storage in lemurs). Therefore, relative to Vatoharanana, the flexibility of energetic strategies employed in Talatakely may be more restricted.

Relatively moderate behavioral adjustments in Talatakely suggest that these animals were less responsive to seasonal changes in the physical environment. During periods of challenge such as fruit scarcity, cross-season trends in *Eulemur rubriventer* behavior were weaker (*e.g.,* significantly less resting in Vatoharanana, no significant change in Talatakely), and may not prepare this population well for winter. Alternatively, strong behavioral or physiological modifications may not be required in this site, but it is reasonable to assume that living in a less productive, less predictable forest (Tecot, Chapter 2) requires at least as much energy partitioning as living where

resources are abundant and seasonal. Weaker modifications may result from less available energy (amount and quality of resources) and higher energetic requirements (distribution of resources in time and space) in this site, resulting in a lower range of solutions available to the animals inhabiting Talatakely. As mentioned above, after a certain point resting may be the only available option (Nash, 1998). The implications of such a strategy are that opportunities for energy storage are more limited (and the need for energy extraction are increased). As energy storage may be the flexible strategy required for this species to reproduce in a habitat with severely reduced predictability of resources (see above), reduced storage opportunities may severely reduce reproductive success in primates (Knott, 1998).

FECAL CORTISOL LEVELS: ENERGY STORAGE AND EXTRACTION STRATEGIES

Cortisol excretion patterns illuminated periods when *Eulemur rubriventer* were challenged in both sites, and combined with time budgets these data were used to infer periods of energetic storage and extraction. Temperature had no effect on *E. rubriventer* fecal cortisol levels, supporting the prediction by Morland (1993) that behavioral adjustments were principally responsible for thermoregulatory adjustments in Lemurids. The dry season was associated with lower cortisol levels and it is suggested here that this relationship is due to the close relationship between rainfall and fruit abundance. Finally, ripe fruit scarcity was the strongest predictor of elevated cortisol levels, demonstrating that fruit scarcity is a period of energetic challenge which is resolved through both behavioral and physiological mechanisms. *Eulemur rubriventer* has an adaptive response to these periods of challenge, and individuals are able to mobilize energy to avoid

undergoing pathological stress. These data strongly support hypotheses suggesting that lemurid primates evolved unique traits which help them avoid stress conferred by Madagascar's environment (Pereira *et al.,* 1999; Wright, 1999).

Energy Partitioning and Lemurid Evolution

These adaptations are reflected in reproductive timing and patterns as well. Weaning in *Eulemur rubriventer* occurs during the austral summer, approximately January through March (Figure 5.1, Table 5.1). Time budgets of *E. rubriventer* during infant weaning indicate that energy was maximized during this critical period (Tecot, Chapter 3), but it is difficult to determine if energy was stored during weaning when food was abundant, since the proportion of time spent feeding and cortisol excretion were variable across years (Figure 5.1).

Inter-annual comparisons enabled analyses of energetic strategies employed during variable combinations of food, reproduction, and climate, and suggest that variable annual strategies may depend upon reproductive burden. This finding may be true for other primate species as well. For example, in 2004 when no infants were weaned, low cortisol levels were coincident with a high proportion of time feeding during fruit abundance, indicating that energy may be stored to prepare for the impending breeding season and winter. In captive lemurs provided with steady provisions, energy is stored during the austral summer, and is essential for winter energy conservation and extraction of energy stores (Pereira *et al.,* 1999). In 2005, however, when all groups were weaning (and carrying) infants, both the proportion of time feeding and cortisol levels were at moderate levels, and may reflect the greater energetic burden of weaning (Figure 5.1). When recovering from reproduction, *E. rubriventer* may adopt a strategy of relative

energy maximization (continuing to rest a small proportion of the time, thus not conserving energy, but traveling little and feeding moderately) and slight energy mobilization (moderately elevated cortisol with fruit abundance) (Table 5.1). In other words, *E. rubriventer* strategies of energy storage and extraction between the austral summer solstice and fall equinox (weaning in all species in Madagascar, Wright, 1999; Lewis and Kappeler, 2005) are flexible, though they are tightly entrained to photoperiod, with appetite changes occurring even in provisioned groups in the United States (Pereira *et al.,* 1999) corresponding to changes in feeding behavior in Madagascar. It is not surprising that energetic requirements are greater when weaning infants are present, but these changes underscore the importance of food abundance at this time for both recovering from the responsibility of providing food for and carrying an infant (in some cases twins), and preparing for the upcoming winter and mating season. When food is not particularly abundant or energy requirements are high during this time, it might be expected that energy storage is prohibited and energy expenditure is intensified, prohibiting reproduction the next season. In fact, despite fruit abundance during weaning no infants were born to any of these groups in 2005.

These results have important implications for considerations of *E. rubriventer* inter-birth intervals as adaptations to this particular environment (see Whitten and Brockman, 2001; Tecot and Overdorff, 2005; Tecot, Chapter 4). Extended interbirth intervals may indicate "bet hedging" (Stearns, 1976), a strategy which saves reproductive effort for times when environmental conditions are optimal. For instance, some species may restrict breeding to years coincident with mast fruiting, and others may avoid breeding in years coincident with mast fruiting because of the reduced likelihood of fruit

abundance the following year when offspring are born (see Ganzhorn *et al.,* 2003b). Bet hedging is often observed in species living in unpredictable habitats, and has been observed in lemurs (Richard *et al.,* 2002; Pochron *et al.,* 2004). Several authors assert that this strategy has been selected for by Madagascar's harsh and unpredictable environment (*e.g.,* Wright, 1999; Richard *et al.,* 2002; Pochron *et al.,* 2004; Dewar and Richard, 2007), and results from this study support this hypothesis.

While austral summer corresponds with weaning, austral fall and winter encompass breeding and gestation in *Eulemur rubriventer.* In early fall ripe fruit was abundant, behavioral strategies maximized energy, and cortisol levels were at their lowest (Figure 5.1), indicating that energy storage may continue into this season, contrary to summer-restricted storage reported by Pereira and colleagues (1999) (Table 5.1). The difference between these two studies is likely attributed to differences in food availability during the 'scarce' season, as captive groups in that study were provisioned, and thus the need to store energy during the fall may be reduced. This finding has great importance for understanding lemur reproduction. As it appears that seasonal reproduction is not dependent upon food fluctuations to initiate breeding in lemurs (Pereira *et al.,* 1999) or other primates (*e.g.,* Sousa *et al.,* 1999), food availability may play a pivotal role in infant survival. For example, as fall transitioned to winter and food availability remained high, behavioral strategies conserved energy (feeding time plunged) and cortisol levels began to rise (Figure 5.1). This period corresponds to energy conservation and mobilization of energy stores in captive lemurs (Pereira *et al.,* 1999), and results from the wild reflect this conservation/extraction strategy (Table 5.1).

But why reduce appetite and mobilize energy stores when food is abundant? Reduced time feeding in the wild may reflect the greater quality of food available at this time, as has been reported widely for primates (Dunbar, 1988; Overdorff, 1988, 1993a, 1996a; Passamini, 1998; Gursky, 2000). But Pereira and colleagues (1999) report reduced *appetite* in lemurs, whereby food was left behind despite year-round consistency in quantity and quality (Table 5.1). Reduced appetite in captivity may merely reflect the situation in the natural environment: fruit abundance during this period may remove the motivation to forage extensively. Additionally, energy mobilization at this time, as indicated by fecal cortisol elevations, may be associated with gestation (Tecot, 2007b). Adult female cortisol levels rise mid-gestation and are likely related to the interaction between the placenta and gravid female as the fetal adrenal glands develop (see Ziegler *et al.,* 2004), rather than in response to environmental stress (Tecot, 2007b). Males respond to these elevations with a slightly later mid-gestation cortisol elevation (Tecot, 2007b), which may result in slightly higher cortisol levels during winter. Further research is necessary to determine whether winter cortisol elevations are indicative of energy mobilization, fetal development (Ziegler *et al.,* 2004; Tecot, 2007b; see Tecot, Chapter 4), or a combination of both.

The austral spring is a critical time during which energy stores are vital. During this time fruit availability was decreasing, time budgets indicate that *Eulemur rubriventer* maximized energy, and cortisol excretion indicates a large degree of energy mobilization (Figure 5.1). Energy mobilization may not be directly related to fruit availability at this time, however. Overdorff *et al.,* (1999) suggested that the austral spring may be a time of energetic stress associated with lactation. During their study of *Eulemur fulvus rufus*, the

austral spring was a time of high fruit abundance (Overdorff *et al.,* 1999). Increased aggression was accompanied by an increase in foraging and feeding upon supplemental food items, indicating competition for resources (Overdorff *et al.,* 1999) and an energy maximization strategy. This was the birth season for both species, and corresponds with the resumption of appetite and the beginning of hair and juvenile growth rate increases in captive lemurs (Table 5.1) (Pereira *et al.,* 1999). These studies suggest that energetic requirements increase due to increased reproductive demands during the austral spring, thus necessitating increased energetic intake. However, although resources were abundant during Overdorff and colleagues' (1999) study, they were also patchy and relatively small (Overdorff, 1996a), and increased energetic demands due to the size and distribution of food patches cannot be ruled out.

Extreme and prolonged cortisol elevations suggest the potential for pathological stress during this time, and may explain why preliminary data indicate that infant mortality in this species occurs within three months of parturition (Tecot and Overdorff, 2005). Such a strong response at this time, coupled with long inter-birth intervals and rapid infant development (Overdorff, 1991; Godfrey *et al.,* 2004), may select for cooperative care in *Eulemur rubriventer*, but further comparisons with other species are necessary. Energy accumulation and conservation during other periods of the year may be crucial for success between the austral spring equinox and summer solstice (September – December) (Pereira *et al.,* 1999).

Disagreement with Pereira *et al.* (1999) lies in assigning importance to these different periods. They assert that lemurid energetic strategies which occur throughout the year exist to conserve and extract energy during the austral winter months, thus

helping lemurs *avoid stress* during winter. This pattern certainly is strongly supported by this study. But this study determined that winter energy conservation was in turn crucial for the following austral spring months when food was scarce. This is clear from phenological data indicating that fruit is scarce (Tecot, Chapter 2), but Pereira *et al.* (1993) note that supplemental items in the diet such as flowers may be more important, as this is when these items peak in abundance. In this study a high percentage of ripe fruit feeding (approximately 90%) occurred during the austral spring despite the presence of flowers, new leaves, and unripe fruit (and the presence of these items was greatest in January, rather than September through December). A large cortisol response indicates that these food items were not sufficient for energetic balance to be maintained without a physiological response. However, the expression, or extent, of a physiological response may in fact depend upon the extent of the availability of these alternative food items. A prolonged (3 month) cortisol peak during the birth season in Vatoharanana (Figure 5.1) suggests that during years when infants are born, the availability of food (stores and in the environment), relative to energetic needs, may be limited. Increased ability to store food earlier in the year, or ingest food from alternative sources at this time of the year, may decrease this prolonged cortisol spike. Nevertheless, energy storage and conservation are critical to energy extraction, and energy maximization is critical to energy extraction and storage.

Therefore, assigning greater importance to periods of storage because of their benefit to periods when energy conservation and extraction occur in tandem does not give credit to such a well-integrated system. Instead, I propose that periods of energy storage and extraction, conservation and maximization, are each key elements enabling the

expression of the others, and ultimately working together to either support or defer reproduction.

Fecal Cortisol and Habitat Disturbance: Site Comparisons

Important site differences in cortisol excretion reflect the behavioral results detailed above, and suggest that, while energetic challenges are resolved through both physiological and behavioral mechanisms, the behavioral and physiological responses to such challenges are limited and weaker in Talatakely, the disturbed habitat. Differences among sites during climate and fruit availability seasons indicated that during times when cortisol levels were highest (*e.g.,* dry and ripe fruit scarcity seasons), fecal cortisol levels in Vatoharanana, the undisturbed forest, were significantly higher; when cortisol levels were lowest (*e.g.,* wet and ripe fruit abundance seasons), fecal cortisol levels were either not significantly different among sites, or tended to be higher in Talatakely, the disturbed forest. These results suggest that during times of challenge only groups in Vatoharanana were able to launch a full behavioral and physiological response, likely because of insufficient energy available in the environment for storage, and later extraction, in Talatakely.

For instance, behavioral strategies were geared towards energy conservation in Talatakely, the disturbed site, with a prolonged period of energy conservation during the fall and winter (Figure 5.2). Extended energy conservation (beginning one month earlier and concluding one month later than in Vatoharanana) may be due to the lack of resources available during the preceding months. While resources were abundant and cortisol levels were low in Vatoharanana during February and March (late austral summer, early austral fall) (Figure 5.1), ripe fruit was almost nonexistent in Talatakely.

In that site during February, the proportion of time spent feeding and cortisol excretion were at their highest (Figure 5.2). While energy was being stored in Vatoharanana, groups in Talatakely were unable to store energy at that time.

Furthermore, no ripe fruit was present in Talatakely in March and groups spent 100% of their time feeding upon unripe guava, *Psidium cattleianum* (Tecot, 2007a). This resource likely buffered the effects of resource scarcity, but it may not have been sufficiently high in quality to provide adequate energy stores for use later in the year, thus resulting in very minor peaks in cortisol, and therefore little energy mobilization (Figure 5.2).

These differences across sites were also reflected in differential reproductive success, as might be expected if energy stores prior to the breeding season are critical for successful reproduction. Infants born to females in the disturbed site experienced 60% infant mortality, while no infant deaths occurred in the undisturbed site (Tecot and Overdorff, 2005). Though no studies of primates have investigated the relationship between cortisol levels and infant survivorship, Pride (2005b) reported that individual (non-infant) mortality was predicted by higher *Lemur catta* cortisol excretion. In view of the results from this study, the same may not be said for infants born to individuals with high cortisol excretion. This discrepancy likely arises from cross-population comparisons conducted in this study. Analyses of cortisol excretion within a single population subject to similar environmental challenges may yield different results. Similarly, the relationship between *Eulemur rubriventer* cortisol and adult survivorship may differ from that in *Lemur catta* since they live in very different societies (multiple adult males and females, strict dominance hierarchy, and high rates of aggression) and

very different habitats (dry forests) (Sauther, 1993; Pereira and Kappeler, 1997; Jolly *et al.,* 2002). Furthermore, it is proposed here that, when comparing populations, higher mean cortisol values in one population compared with the other are not directly indicative of heightened energetic challenge, or stress.

While long-term trends of cortisol excretion were similar in each site, important differences were evident. The magnitude and duration of peaks were greater in Vatoharanana, the undisturbed forest, contrary to expectations and other studies of primate cortisol excretion in relation to habitat disturbance (Cavigelli, 1999; Chapman *et al.,* 2006; Martinez-Mota *et al.*, 2007). The results of this study suggest that, similar to some salamander and bird species (Homan *et al.,* 2003; Cyr and Romero, 2007), animals in Talatakely were unable to launch a full physiological response, and principally relied upon behavioral mechanisms. This result may occur because these individuals were excessively stressed, or because more sensitive individuals were selected out of the population (Romero, 2004). Narrower peaks in cortisol excretion suggest that the Talatakely population may employ a strategy whereby glucocorticoids are only mobilized during the most intensive periods (*e.g.,* at the height of fruit scarcity), and are not sustained for the duration of the challenge. *E. rubriventer* can then avoid sustained elevations in glucocorticoid levels throughout the entirety of the adverse conditions, and thus avoid the detrimental fitness effects of long-term exposure (*e.g.,* inhibited reproduction and immune function) (Sapolsky, 1987). However, how such a strategy may impact the ability of this species to cope with other types of stressors has yet to be determined.

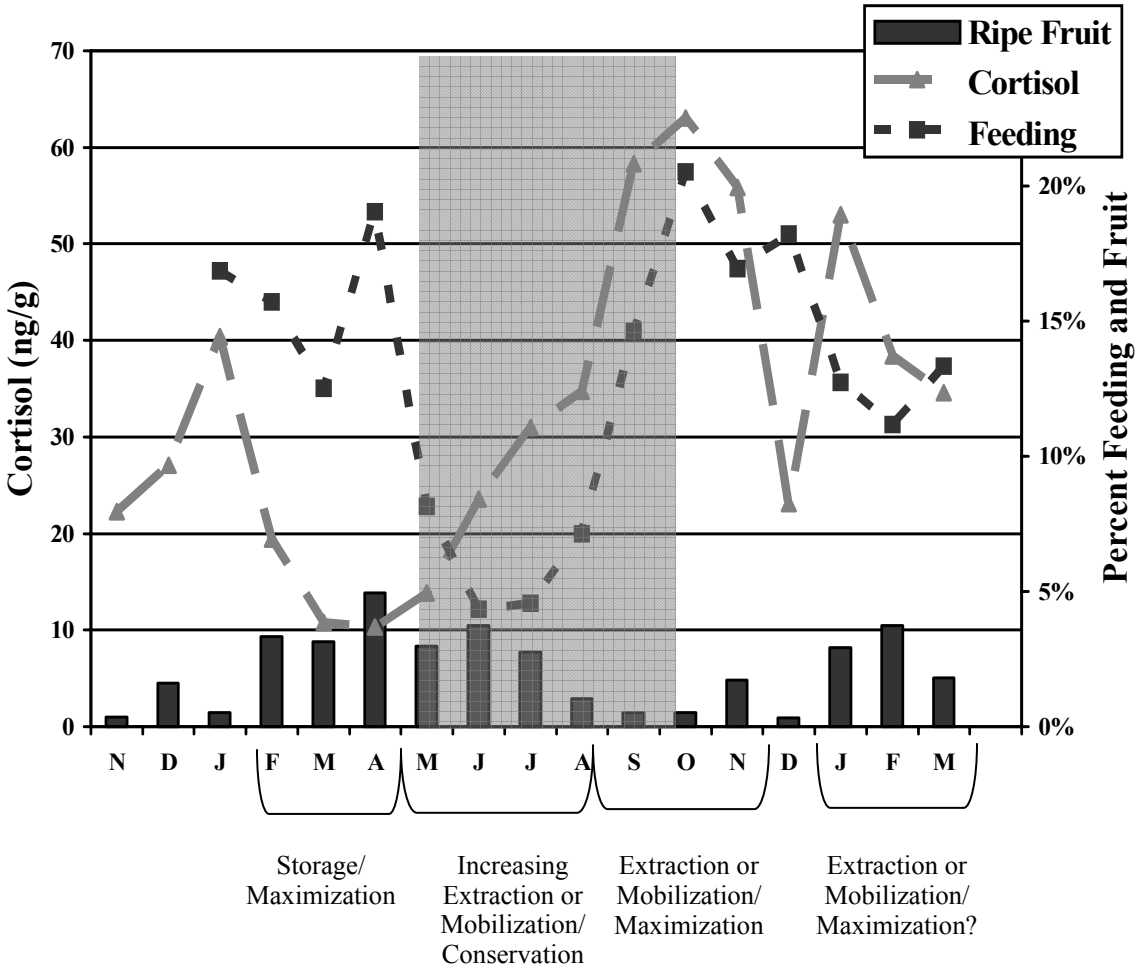

Figure 5.1. Monthly ripe fruit feeding, phenology, cortisol levels, and energetic strategies as they relate to reproductive seasons throughout the study, in Vatoharanana. Shaded area denotes the range of peak gestation. Month is on the x-axis, from November 2003 through March, 2005.

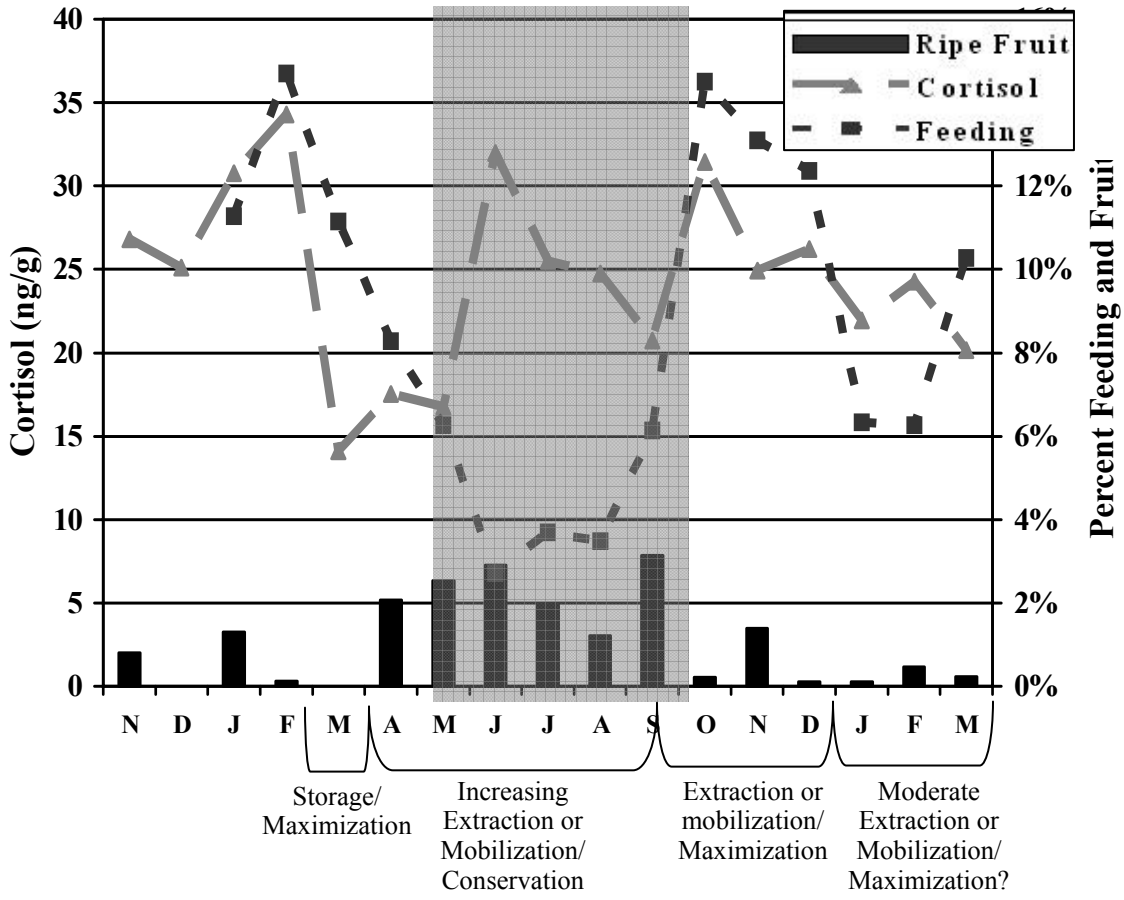

Figure 5.2. Monthly ripe fruit feeding, phenology, cortisol levels, and energetic strategies as they relate to reproductive seasons throughout the study, in Talatakely. Shaded area denotes the range of peak gestation. Month is on the x-axis, from November 2003 through March, 2005.

Table 5.1. Seasonal behavioral and physiological mechanisms employed by lemurid (*Eulemur* and *Lemur*) primates. Variables below the bold line were collected during this study, and are reported for Vatoharanana. Those above the line were reported in Pereira *et al.*, 1999, and months have been adjusted to correspond to the southern hemisphere.

Month	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Appetite	Full			Decreasing		Lowest				Increasing		Full
Juvenile Growth	Growth			Low Growth Rates					Growth			
Hair Growth	Growth				Low Growth Rates					Growth		
IGF-1 and T4[1]	Low: Storage			High: Extraction								Low: Storage
Subcutaneous Fat	High					Low				Brief Elevations		High
Season (Austral)	Summer			Fall		Winter			Spring			Summer
Ripe Fruit Phenology	Low to High Variable		High					Low			Med	Low-Med Variable
Temperature	Warm				Cold						Warm	
Rainfall	Wet				Dry							Wet
Behavior Strategy	Moderate Maximization		Maximization			Conservation			Maximization			Moderate Maximization
Reproduction	Late Weaning			Pre-breeding		Gestation			Birth		Lactation/Early Weaning	
Cortisol	Med-High		Med-Low	Low			Rising Low to High[3]		High			Med-Low
Storage and Extraction[2]	**Moderate Extraction (Variable)**		**Storage**			**Extraction?**[3]			**Extraction**			**Storage?**

[1] Metabolic hormones. These signify the range of opportunities for energy storage and extraction as found in captive, provisioned lemurs.
[2] Strategies that might be used according to the combination of data from these studies.
[3] Elevations may be due to the development of the transitional zone of the fetal adrenal glands, interaction between mother and fetus, and consequent elevations in other group members (Tecot, 2007b).

CONSERVATION ENDOCRINOLOGY

Field endocrinology has emerged as a reliable tool that is advantageous because it does not inflict additional stress associated with capture and venipuncture, and can be used to study species in the natural environment where they evolved (Dettmer *et al.,* 1996; Bronson, 1999; Whitten *et al.,* 1998a; Strier and Ziegler, 2005; Tarlow and Blumstein, 2007). This technique is useful for answering questions about selection pressures (Strier *et al.,* 1999; Whitten *et al.,* 1998b), which would normally require several decades of research in long-lived species (Pride, 2005b). For conservation purposes, field endocrinology can be an invaluable early warning signal of population decline (Pride, 2005b; Chapman *et al.,* 2007), and a powerful tool for monitoring wild populations for conservation management (Hofer and East, 1998). Utilizing field endocrinology techniques for conservation purposes has recently been termed "conservation endocrinology" (Cockrem, 2005).

Conservation endocrinology has been used widely to determine whether anthropogenic disturbances are stressful (Cockrem, 2005), such as collars (Creel *et al.,* 1997) and capture protocols (Morton *et al.,* 1995) used by researchers, and the presence of oil wells (Sayre, 1996), pollution (Norris *et al.,* 1999), and tourists (Romero and Wikelski, 2002; Walker *et al.,* 2005, 2006) in the natural habitat. Hormonal profiles can also assist in captive breeding colony management by identifying limits to (Hendrie *et al.,* 1996), or requirements for (Mendoza and Mason, 1991), reproduction, thus facilitating successful breeding. They can help identify individuals or populations who may be amenable to reintroduction into the wild, or translocation if a forest is threatened.

Clearly in this study, the endocrinology results have show that, relative to groups in Talatakely, the Vatoharanana population would be better suited to translocation into another forest should the need arise since they were able to launch an adaptive behavioral and physiological response to environmental pressures.

Conservation endocrinology can also be used to identify optimal and suboptimal times for changes such as social group manipulation, construction, or translocations, and monitor species after such modifications have been implemented (Goymann *et al.,* 1999; Waas *et al.,* 1999; Marín *et al.,* 2006; Edward Louis, personal communication). However, recommendations cannot be based merely upon one parameter. Fecal cortisol fluctuations in *Eulemur rubriventer* indicate that the period from March through May is ideal for intervention (Figures 5.1 and 5.2). Yet, low cortisol levels at this time are part of a suite of responses which serve to store energy for successful reproduction in the following months (Table 5.1), and thus human conservation activities during the period of lowest cortisol levels may not be beneficial, and may even be harmful.

Early captive research has provided a vast foundation on which to build knowledge of the interaction between species and the wild environment (Romero, 2004). As conservation endocrinology develops and advances (Whitten *et al.,* 1998a; Walker *et al.,* 2005; Ziegler and Wittwer, 2005) it becomes increasingly important to conduct basic yet thorough studies to establish a theoretical framework for habitat and population assessment, as current theory is based largely on research with captive animals (Romero, 2004). Noninvasive techniques have been developed which facilitate such research (Whitten *et al.,* 1998a; Ziegler and Wittwer, 2005), and noninvasive cortisol studies in wild primates have been conducted over the past decade (*e.g.,* Whitten *et al.,* 1998b;

Cavigelli, 1999; Strier *et al.,* 1999). However, studies of the ecological correlates to cortisol excretion are minimal, and the use of field endocrinology in studying the effects of habitat disturbance is just beginning in vertebrates. Therefore, what we know of the relationship between habitat disturbance and cortisol excretion in primates is severely limited.

While some studies suggest that populations in disturbed habitats excrete higher levels of cortisol (Martinez-Mota *et al.,* 2007; Chapman *et al.,* 2006), which are thus indicative of a more stressed population, this study found that animals in a stressed environment may have a muted response. To this end, the results of this study are significant. It is exceedingly important to recognize that low levels of cortisol do not necessarily indicate a stress-free state. On the contrary, individuals with a substantial stress response may be best equipped to deal with stressors, such as new environments brought on by conservation initiatives (*e.g.,* translocations, reintroductions, tourism, trail maintenance), or, unfortunately, special interests (*e.g.,* harvesting, prospecting).

Recommendations for Talatakely

The situation in Talatakely may be critical. Although pathologically elevated cortisol levels may have an impact upon long-term survival functions such as reproduction (Sapolsky, 1985, 1992; Wasser and Starling, 1988; Mendoza and Mason, 1988; Chatterton *et al.,* 1991; Arnold and Dittami, 1997; Cameron, 1997; Bronson, 1999), immune function (Cohen, 1988; Esch *et al.,* 1975; Keller *et al.,* 1983; Laudenslager *et al.,* 1983; Muehlenbein, 2006), mortality (Colwell *et al.,* 1988; Rodway *et al.,* 1996; Cotter and Gratto, 1995; Pride, 2005b), and longevity (Burrows *et al.,* 1994), a severely muted hormonal and behavioral response to known environmental challenges,

coupled with a high rate of infant mortality (Mittermeier *et al.,* 2006; Tecot, this study) and highly unpredictable resources (Tecot, Chapter 2), indicates that this population may be at risk of declining. Population numbers of sympatric species in Talatakely are dwindling (P. Wright, personal communication), and management decisions in the near future may be crucial to the survival of the Talatakely *Eulemur rubriventer* population.

Ranomafana, established as a national park in 1986 (Wright, 1992; Wright and Andriamihaja, 2002) is the 3rd most visited park in Madagascar (Association Nationale pour la Gestion des Aires Protègées (ANGAP), personal communication). Every year the number of tourists in Ranomafana increases (3,256 tourists in 1994, 13,145 tourists in 2000, and 16,222 tourists in 2006; ANGAP, personal communication) and a large majority of these visit Talatakely. As numbers of tourists increase, the size of tourist groups increase, thus subjecting small groups of *Eulemur rubriventer* to high levels of admiration, which include noise, photography, and restricted routes of escape. Fortunately, ANGAP has instituted a ban on flash photography, but limits on the number of tourists per guide do not reduce the number of people viewing animals at a single time, as large groups remain cohesive despite the increase in tourist guides (Tecot, personal observation). Animals may be indirectly affected by tourists as well, as an increase in the number of tourists annually necessitates trail maintenance and construction.

Although tourists are likely not the reason for different cortisol profiles in Talatakely, tourist presence is concentrated around the months of July through October (ANGAP, personal communication), which is coincident with late gestation and birth in *Eulemur rubriventer*, and lowering resource availability in Talatakely. In Vatoharanana this is when cortisol levels are highest, indicating that this is when energy stores are extracted. If tourism presence increases activity (*e.g.,* lemurs travel higher in trees or farther to avoid people), or decreases feeding time, this could prove to be a dangerous

drain on energy which, combined with unpredictable resources, may affect infant survival (though this remains to be tested). In fact, though adult Megellanic penguins *(Spheniscus magellanicus)* habituated to tourist presence, unfledged Megellanic penguin and hoatzin *(Opisthocomus hoazin)* chicks' glucocorticoid responses to tourists were highly sensitive (Müllner *et al.,* 2004; Walker *et al.,* 2005), and hoatzin chicks living in areas with tourists suffered reduced survival (Müllner *et al.,* 2004). Certainly reduced *Eulemur rubriventer* infant survival in Talatakely compared with Vatoharanana supports this hypothesis, but further study of the acute response to stress (*i.e.,* reactivity), particularly in sub-adults, would provide the necessary data to test whether this population is truly sensitive to tourist presence.

Income generated from tourists directly benefits people surrounding the park boundaries, as well as the flora and fauna inside the park, so banning tourists in Talatakely is not desirable. Reductions in noise and greater enforcement of the number of tourists per animal group, as has been instituted with the critically endangered *Prolemur simus* (ANGAP, personal communication), might be instituted. Furthermore, tourists have been prevented altogether from viewing *Prolemur simus* upon the birth of infants (ANGAP, personal communication), and this policy might be implemented for other species in the park as well. Limiting tourists to main trails will reduce seedling trampling and encourage recruitment of important tree species. Tourist congestion in Talatakely has been slightly alleviated with the development of Vatoharanana as a tourist site, but as tourist numbers increase every year this is not a satisfactory solution. Furthermore, care should be taken to habituate Vatoharanana groups to human presence and noise in areas newly frequented by tourists.

Should the need arise to take radical conservation action in the future, translocations might be feasible mid-March if substantial provisioning is implemented

through May. This should provide ample food for energy storage and counterbalance stress associated with transport. However, translocation is extreme, more research is necessary to determine the feasibility and long-term effects of this process, and it is not recommended for this population of *Eulemur rubriventer* at this point.

Conclusions

This study is the first to systematically compare fecal cortisol levels across seasons, years, and habitats in conjunction with detailed phenological and climatological data in a wild primate. The implications of this study are two-fold, as they apply to models of lemur evolution and conservation.

MODELS OF LEMUR EVOLUTION

Opportunities for energy storage are scarce in Madagascar, and adaptations supporting energy storage may have been crucial for lemur reproduction and survival in a dynamic environment with unpredictable resources. This study demonstrates a robust association between fruit availability and both physiological and behavioral energetic strategies, and a moderate association between climate and energy partitioning. These results strongly support hypotheses which state that Madagascar's harsh environment selected for various distinguishing lemurid traits which conserve and maximize energy to avoid stress (Jolly, 1984; Sauther, 1993; Tilden and Oftedal, 1995; Overdorff *et al.,* 1999; Pereira *et al.,* 1999; Wright, 1999; Godfrey *et al.,* 2004). I suggest an elaboration of this hypothesis which states that energy conservation and maximization facilitate energy storage (Richard *et al.,* 2000) and subsequent extraction.

Though reproduction *per se* is not more energetically expensive in lemurs than in other primates, it may be more constrained by Madagascar's environment as opportunities for energy storage are minimal. Fruit scarcity may last as long as six months (Wright *et al.,* 2005), and reduce the window of reproductive opportunity, resulting in highly seasonal, synchronized breeding (Wright, 1999). While the most expensive reproductive stages are timed with the highest likelihood of food abundance (Wright, 1999), as in other primate species (Altmann, 1980; van Schaik and van Noordwijk, 1985; Di Bitetti and Janson, 2000) and obligate breeding vertebrates in general (Lack, 1950; Bronson, 1995), the result of this schedule is that the most potentially stressful times are those which are necessarily *not* timed with food abundance: birth and early lactation.

Success depends largely upon storage opportunities earlier in the year. Recovery time between weaning and mating in large-bodied lemurs is restricted to a few months during variable fruit availability from year-to-year. If energy storage during that time is minimal or absent, reproduction may be deferred until the environment is optimal or energy has been stored. Otherwise, birth/early lactation stress can have severe consequences. In fact, folivorous *Propithecus verreauxi* are similarly affected by a lack of energy storage opportunities prior to the birth season: individuals below a certain body mass threshold are not able to reproduce (Richard *et al.,* 2000). Variation in the ability to store energy prior to the birth season will have greatest influence upon infant survival.

Inter-site comparisons support the hypothesis that energy storage is required for reproduction in lemurs, with greatest site disparities in available energy occurring during the end of the austral summer when energy is stored (Pereira *et al.,* 1999), and greatest

site disparities in cortisol occurring around the birth season. Only the Vatoharanana population stored energy, and while cortisol levels elevated in both sites during the birth season, only slight elevation occurred in Talatakely, indicating only slight extraction of energy. Extremely high infant mortality in Talatakely (Appendix 3) indicates that the inability to store energy resulted in an inability to mobilize energy when necessary for successful reproduction.

CONSERVATION

Finally, I found that Talatakely, the disturbed habitat, is really quite a difficult environment in terms of providing ample energy to support survival and reproduction. The availability of food is not associated with climate, and food is scarce and highly unpredictable month to month and year to year. This population's response to such extreme environmental challenge was relatively weak. As an already excellent economizer of energy, sleeping for extended periods of time (Overdorff, 1993a; Tecot, 2006), *Eulemur rubriventer* in this extremely unpredictable site may have reached the threshold of their flexibility. Results from this study suggest that energy in the disturbed environment places an upper limit on strategies of energy maximization and storage, and therefore energy extraction. These results are of particular significance for those investigating the effects of habitat disturbance or the viability of a population as indicated by fecal corticoids, and highlight the importance of conducting systematic, long-term ecological studies in combination with studies of energy partitioning.

Directions for Future Research

Models of Lemurid Evolution

Studies of primate energetics have important implications for evaluating models of lemurid evolution. This study established periods when physiological and behavioral mechanisms were used to cope with environmental change. Measures of the impact of stress on individuals such as parasite load and diversity, collected simultaneously with hormonal and behavioral data, may help distinguish between periods when these mechanisms help individuals cope with stress, and when they represent the pathology of the stress response. Endoparasites were collected during this study from each individual in each site across seasons and years, and analyses are currently underway.

Behavioral analyses of time budgets represent a crude measurement of energy intake and energy expenditure. Analyses of feeding behavior, such as dietary diversity, species exploited, and nutritional content of food items, enable further analysis of the impact of varying food availability upon *Eulemur rubriventer.* Phytochemical analyses in particular provide a quantitative measure of caloric intake, thus providing better indices of gross energy (Coelho, 1986). Studies of ranging behavior would further help identify spatial constraints on energy accumulation and requirements for energy expenditure during varying periods of food abundance.

Doubly-labelled water has been proven a more reliable indicator of energy expenditure than time budgets (Weathers and Nagy, 1980). Tests can be conducted in free-ranging animals through urine collection once the doubly-labelled water has been administered (Weathers and Nagy, 1980), and has been used to measure energy expenditure in free-ranging mouse lemurs (see Ganzhorn *et al.,* 2003b). Measures of

energy expenditure can provide accurate measures of metabolic costs to activity overall and across seasons, and recording changes in field metabolism in *Eulemur rubriventer* would be particularly interesting because of their extended resting bouts, low resting metabolic rates (Snodgrass *et al.,* 2007) and their phylogenetic proximity to species which regularly enter torpor.

Finally, investigations of *Eulemur rubriventer* reproduction in a captive setting would benefit studies interested in how lemur reconcile the competing needs of survival and reproduction. Mating has not been observed in this species in the wild (Overdorff, personal communication) so at the most basic level it remains unknown whether mating occurs during years when infants are not born, and whether infants born late are pre- or full-term. Longitudinal studies of infant survivorship and estimations of the rate and timing of fetal loss will help determine when and what selective factors influence infant mortality, and whether high infant mortality observed in Talatakely was anomalous or characteristic of this population.

Lemur Conservation

The results of this study may also be employed in future conservation efforts. By establishing profiles of cortisol excretion by *Eulemur rubriventer* in different ecological matrices, this study provided a baseline and an ecological context within which fecal cortisol levels from this species in other habitat types may be viewed. The next step is to determine the long-term impacts of these cortisol profiles on reproductive success so that projections can be made for populations living in other habitats.

References

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Arnold, W. and Dittami, J. 1997. Reproductive suppression in male alpine marmots. *Animal Behaviour*. 53(1):53-66.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Atsalis S. 1999b. Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *International Journal of Primatology*. 20:883-910.

Bollen, A. and Donati, G. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*. 37(1):32-43.

Brockman, D.K. and van Schaik, C.P. 2005. Seasonality and reproductive function. In: D.K. Brockman, C.P. and van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 269-305.

Bronson, F.H. 1995. Seasonal variation in human reproduction: Environmental factors. *The Quarterly Review of Biology*. 70(2):141-164.

Bronson, F.H. 1999. Puberty and energy reserves: a walk on the wild side. In: K. Wallen and J. E. Schneider, editors. *Reproduction in Context*. Cambridge: MIT Press. Pp. 15-34.

Bronson, F.H. and Heideman, P.D. 1994. Seasonal regulation of reproduction in mammals. In: E. Knobil and J. D. Neil, editors. *The Physiology of Reproduction, 2nd ed*. New York: Raven Press.

Burrows, R., Hofer, H., East, M.L. 1994. Demography, extinction and intervention in a small population: The case of the Serengeti wild dogs. *Proceedings of the Royal Society of London Series B*. 256:281-292.

Cameron, J.L. 1997. Stress and behaviorally induced reproductive dysfunction in primates. *Seminars in Reproductive Endocrinology*. 15(1):37-45.

Cavigelli, S.A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*. 57(4):935-944.

Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.L., Saj, T.L., Ziegler, T.E. 2006. Do food availability, parasitism, and stress have synergistic effects on Red Colobus populations living in forest fragments? *American Journal of Physical Anthropology*. 131:525-534.

Chapman, C.A., Saj, T.L., Snaith, T.V. 2007. Temporal dynamics of nutrition, parasitism, and stress in Colobus monkeys: Implications for population regulation and conservation. *American Journal of Physical Anthropology*. 134(2):240-250.

Chatterton, R.T., Kazer, R.R., Rebar, R.W. 1991. Depletion of luteal phase serum progesterone during constant infusion of cortisol phosphate in the cynomolgus monkey. *Fertility and Sterility*. 56:547-554.

Cockrem, J.F. 2005. Conservation and behavioral neuroendocrinology. *Hormones and Behavior*. 48(4):492-501.

Coelho, A.M. 1986. Time and energy budgets. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology*. New York: Alan R. Liss. Pp. 141–166.

Cohen, S. 1988. Psychosocial models of the role of social support in the etiology of physical disease. *Health Psychology*. 7:269-297.

Colwell, M.A., Gratto, C.L., Oring, L.W., Fivizzani, A.J. 1988. Effects of blood sampling on shorebirds: Injuries, return rates and clutch desertions. *Condor*. 90:942-945.

Cotter, R.C. and Gratto, C.J. 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. *Journal of Wildlife Management*. 59:93-98.

Creel, S., Creel, N.M., Monfort, S.L. 1997. Radiocollaring and stress hormones in African wild dogs. *Conservation Biology*. 11:544-548.

Cyr, N.E. and Michael Romero, L. 2007. Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *General and Comparative Endocrinology*. 151(1):82-89.

Dausmann, K., Glos, J., Ganzhorn, J.U., Heldmaier, G. 2004. Hibernation in a tropical primate. *Nature*. 429:825-826.

Dettmer, E.L., Phillips, K.A., Rager, D.R., Bernstein, I.S., Fragaszy, D.M. 1996. Behavioral and cortisol responses to repeated capture and venipuncture in *Cebus apella*. *American Journal of Primatology*. 38(4):357-362.

Dewar, R.E. and Richard, A.F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences*. 104(34):13723-13727.

DiBitetti, M.S. and Janson, C.H. 2000. When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*. 50:109-130.

Dunbar, R.I.M. 1988. *Primate Social Systems*. Ithaca, New York: Cornell University Press.

Eger, J.L., Mitchell, L. 2003. Chiroptera, Bats. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1287-1298.

Esch, G.W., Gibbons, J.W., Bourque, J.E. 1975. An analysis of the relationship between stress and parasitism. *American Midland Naturalist*. 93(2):339-353.

Ganzhorn, J.U., Klaus, S., Ortmann, S., Schmid, J. 2003b. Adaptations to seasonality: Some primate and nonprimate examples. *Primate Life Histories and Socioecology*. Chicago: University of Chicago Press. Pp. 132.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*. 123:250-276.

Gould, L., Sussman, R.W., Sauther, M.L. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*. 120(2):182-194.

Goymann, W., Möstl, E., Van't Hof, T., East, M.L., Hofer, H. 1999. Noninvasive fecal monitoring of glucocorticoids in spotted hyenas, *Crocuta crocuta*. *General and Comparative Endocrinology*. 114(3):340-348.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Gursky, S. 2000. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*. 21:477-495.

Hemingway, C.A. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edward's sifaka, *Propithecus diadema edwardsi,* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 17:637-657.

Hemingway, C.A. 1999. Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? *Behavioral Ecology and Sociobiology*. 45:311-322.

Hendrie, T.A., Peterson, P.E., Short, J.J., Tarantal, A.F., Rothgarn, E., Hendrie, M.I., Hendrickx, A.G. 1996. Frequency of prenatal loss in a macaque breeding colony. *American Journal of Primatology*. 40(1):41-53.

Hofer, H. and East, M.L. 1998. Biological conservation and stress. In: A.P. Møller, M. Milinski and P.J.B. Slate, editors. *Advances in the Study of Behavior, Vol. 27*. San Diego: Academic Press. Pp. 405-525.

Homan, R.N., Regosin, J.V., Rodrigues, D.M., Reed, J.M., Windmiller, B.S., Romero, L.M. 2003. Impacts of varying habitat quality on the physiological stress of spotted salamanders *(Ambystoma maculatum)*. *Animal Conservation*. 6(1):11-18.

Irwin, M.T. 2007. Living in forest fragments reduces group cohesion in Diademed Sifakas *(Propithecus diadema)* in Eastern Madagascar by reducing food patch size. *American Journal of Primatology*. 69:434-447.

Janson, C. and Verdolin, J. 2005. Seasonality of primate births in relation to climate. In: D.K. Brockman, and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 307-350.

Johnson, B.K. 2002. *Soil Characterization and Reconnaissance Survey of the Ranomafana National Park Area, Southeastern Madagascar* [Doctoral Dissertation]. Raleigh, NC: North Carolina State University.

Jolly, A. 1984. The puzzle of female feeding priority. In: M. Small, editor. *Female Primates: Studies by Women Primatologists*. New York: Alan R. Liss. Pp. 197-215.

Jolly, A., Dobson, A., Rasamimanana, H.M., Walker, J., O'Connor, S., Solberg, M., Perel, V. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *International Journal of Primatology*. 23(2):327-353.

Keller, S.E., Weiss, J.M., Schleifer, S.L., Miller, N.E., Stern, M. 1983. Stress-induced suppression of immunity in adrenalectomized rats. *Science*. 221:1301-1304.

Knott, C.D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*. 19:1061-1079.

Lack, D. 1950. The breeding seasons of European birds. *Ibis*. 92:288-316.

Laudenslager, M.L., Ryan, S.M., Drugan, R.C., Hyson, R.L., Maier, S.F. 1983. Coping and immunosuppression: Inescapable but not escapable shock suppresses lymphocyte proliferation. *Science*. 221:568-570.

Lewis R.J., and Kappeler P.M. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*. 67*:*347-364.

Lyman, C.P., Willis, S.S., Malan, A., Wang, L.C.H. 1982. *Hibernation and Torpor in Mammals and Birds*. London: Academic Press.

Marín, C., Honess, P., Ramíreza, M.J. 2006. Physiological and behavioural study after translocation of a breeding colony of Rhesus Macaques *(Macaca mulatta)*. *Folia Primatologica*. 77(4):319-320.

Martínez-Mota, R., Valdespino, C., Sánchez-Ramos, M.A., Serio-Silva, J.C. 2007. Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Animal Conservation*. 10:374-379.

Mendoza, S.P. and Mason, W.A. 1988. Behavioral and endocrine consequences of heterosexual pair formation in squirrel monkeys. *Physiology and Behavior*. 46:597-603.

Mendoza, S.P. and Mason, W.A. 1991. Breeding readiness in squirrel monkeys: female-primed females are triggered by males. *Physiology and Behavior*. 49(3):471-479.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersall, I., Meyers, D.M. 2006. *Lemurs of Madagascar. 2nd Edition*. Washington, DC: Conservation International.

Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., Zipparro, V.B. 2000. Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*. 32(4b):811-823.

Morland, H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 193-203.

Morton, D.J., Anderson, E., Foggin, C.M., Kock, M.D., Tiran, E.P. 1995. Plasma cortisol as an indicator of stress due to capture and translocation in wildlife species. *Veterinary Record*. 136(3):60-63.

Muehlenbein, M.P. 2006. Intestinal parasite infections and fecal steroid levels in wild chimpanzees. *American Journal of Physical Anthropology*. 130:546-550.

Müllner, A., Linsenmair, K.E., Wikelski, M. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks *(Opisthocomus hoazin)*. *Biological Conservation*. 118(4):549-558.

Nash, L.T. 1998. Vertical clingers and sleepers 1: Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*. 69(Suppl. 1):204-217.

Negus, N.C. and Berger, P.J. 1972. Environmental factors and reproductive processes in mammalian populations. In: J.T. Velardo and B.A. Kasprow, editors. *Biology of Reproduction: Basic and Clinical Studies*; *Third Pan American Congress on Anatomy*, New Orleans. Pan American Association of Anatomy: Pp. 89-98.

Nicoll, M.E. 2003. *Tenrec ecaudatus,* Tenrec, *Tandraka, Trandraka*. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1283-1287.

Norris, D.O., Donahue, S., Dores, R.M., Lee, J.K., Maldonado, T.A., Ruth, T., Woodling, J.D. 1999. Impaired adrenocortical response to stress by brown trout, *Salmo trutta*, living in metal-contaminated waters of the Eagle River, Colorado. *General and Comparative Endocrinology*. 113(1):1-8.

Overdorff, D.J. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D.J. 1991. *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral dissertation]. Durham: Duke University. 313 p.

Overdorff, D.J. 1993a. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur* fulvus rufus in the Ranomafana-National-Park, Madagascar. International Journal of Primatology. 14(5):721-753.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40(4):327-342.

Overdorff, D.J., Merenlender, A.M., Talata, P., Telo, A., Forward, A.Z. 1999. Life history of *Eulemur fulvus rufus* from 1988-1997: Implications for ecological stress in southeastern Madagascar. *American Journal of Physical Anthropology.* 108:295-310.

Passamini, M. 1998. Activity budget of Geoffroy's Marmoset *(Callithrix geoffroyi)* in an Atlantic forest in Southeastern Brazil. *American Journal of Primatology*. 46:333-340.

Pereira, M.E. and Kappeler, P.M. 1997. Divergent systems of agonistic behavior in Lemurid primates. *Behaviour*. 134:225–274.

Pereira, M.E., Russ, A.S., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Publishers.

Petter-Rousseaux, A. 1980. Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In: P. Charles-Dominique, Cooper, H.M., Hladik, A., Hladik, C.M., Pages, E., Pariente, G.F., Petter-Rousseaux, A., Petter, J.-J., Schilling, A., editor. *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*. New York: Academic. Pp. 137-152.

Pochron, S.T., Tucker, W.T., Wright, P.C. 2004. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 125:61-72.

Pride, E. 2005a. Optimal group size and seasonal stress in ring-tailed lemurs *(Lemur catta)*. *Behavioral Ecology*. 16(3):550-560.

Pride, E. 2005b. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs *(Lemur catta)*. *Biological Letters*. 1:60-63.

Raselimanana, A.P. 2003. Gerrhosauridae, Plated Lizards. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 978-983.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*. 39(4):381-391.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Rodway, M.S., Montevecchi, W.A., Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic puffins *(Fratercula arctica)*. *Biological Conservation*. 76:311-319.

Romero, L.M. 2004. Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*. 19(5):249-255.

Romero, L.M. and Wikelski, M. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galapagos marine iguanas. *Biological Conservation*. 108(3):371-374.

Sapolsky, R.M. 1985. Stress-induced suppression of testicular function in the wild baboon: Role of glucocorticoids. *Endocrinology*. 116:2273-2278.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons. In: D. Crews, editor. *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*. Englewood Cliffs, New Jersey: Prentice Hall. Pp. 291-322.

Sapolsky, R.M. 1992. *Stress, the Aging Brain, and the Mechanisms of Neuron Death*. Cambridge: MIT Press.

Sauther, M.L. 1993. Resource competition in wild populations of ringtailed lemurs *(Lemur catta)*: Implications for female dominance. In: P. M. Kappeler and J. U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum. Pp. 135–152.

Sayre, R.W. 1996. *Ecology of Bighorn Sheep in Relation to Habitat and Oil* [Doctoral Dissertation]: University of North Dakota. 138 p.

Schmid, J., Kappeler, P.M. 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur *(Microcebus murinus)*. *Behavioural Ecology and Sociobiology*. 43:125-132.

Schmid, J. and Stephenson, P.J. 2003. Physiological adaptations of Malagasy mammals: Lemurs and tenrecs compared. In: S.M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1198-1203.

Sørg, J.-P. and Røhner, U. 1996. Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. *Primate Report*. 46(1):57-80.

Sørg, J.-P., Ganzhorn, J.U., Kappeler, P.M. 2003. Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestiere. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1512-1519.

Sousa, M., Peregrino, H., Cirne, M., Mota, M. 1999. Reproductive patterns and birth seasonality in a South-American breeding colony of common marmosets, *Callithrix jacchus*. *Primates*. 40(2):327-336.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review in Biology*. 51:3-47.

Stephenson, P.J. 2003. Lipotyphla (ex Insectivora): *Geogale aurita,* Large-eared tenrec. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1265-1273.

Strier, K.B. and Ziegler, T.E. 2005. Advances in field-based studies of primate behavioral endocrinology. *American Journal of Primatology*. 67(1):1-4.

Strier, K.B., Ziegler, T.E., Wittwer, D.J. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis *(Brachyteles arachnoides)*. *Hormones and Behavior*. 35:125-134.

Tarlow, E.M. and Blumstein, D.T. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*. 102(3-4):429-451.

Tecot, S. 2006. Activity budget and microhabitat in *Eulemur rubriventer*. *American Journal of Primatology*. 68(1):111-112.

Tecot, S. 2007a. Seasonality, phenology, and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. S44:230.

Tecot, S. 2007b. Fecal cortisol levels and maintenance behaviors in wild groups of a cooperatively breeding species, the red-bellied lemur *(Eulemur rubriventer)*. *American Journal of Primatology*. 69(1):127.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Tilden, C.D. and Oftedal, O.T. 1995. The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: L Alterman, GA Doyleand MK Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 119-131.

van Schaik, C., and van Noordwijk, MA. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques *(Macaca fascicularis)*. *Journal of Zoology*. 206:533-549.

Waas, J.R., Ingram, J.R., Matthews, L.R. 1999. Real-time physiological responses of red deer to translocations. *Journal of Wildlife Management*. 63(4):1152-1162.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2005. Field endocrinology and conservation biology. *Integrative and Comparative Biology*. 45(1):12-18.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2006. Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology*. 20(1):146-154.

Wang, L.C.H. 1989. Ecological, physiological and biochemical aspects of torpor in mammals and birds. In: L.C.H. Wang, editor. *Advances in Comparative and Environmental Physiology*. Berlin: Springer-Verlag. Pp. 361–401.

Wasser, S.K. and Starling, A.K. 1988. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology*. 16(2):97-121.

Weathers W.W., and Nagy K.A. 1980. Simultaneous Doubly Labeled Water (3hh18o) and time-budget estimates of daily energy-expenditure in *Phainopepla nitens*. Auk. 97:861-867.

Whitten, P.L. and Brockman, D.K. 2001. Strepsirrhine Reproductive Ecology. In: P.T. Ellison, editor. *Reproductive ecology and human evolution*. New York: Aldine de Gruyter. Pp. 321-350.

Whitten, P.L., Brockman, D.K., Stavisky, R.C. 1998a. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*. Pp. 1-23.

Wright, P.C. 1992. Primate ecology, rainforest conservation and economic development: Building a National Park in Madagascar. *Evolutionary Anthropology*. 1:25-33.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*. 42:31-72.

Wright, P.C. and Andriamihaja, B. 2002. Making a Rain Forest National Park Work in Madagascar: Ranomafana National Park and Its Long-term Research Commitment. In: J. Terborgh, C. van Schaik, L. Davenport and M. Rao, editors. Making Parks Work: Strategies for Preserving Tropical Nature. Washington: Island Press. Pp. 112-136.

Wright, P.C. and Martin, L.B. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: L. Alterman, G.A. Doyle and M.K. Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum. Pp. 45-60.

Ziegler, T.E. and Wittwer, D.J. 2005. Fecal steroid research in the field and laboratory: Improved methods for storage, transport, processing, and analysis. *American Journal of Primatology*. 67(1):159-174.

Ziegler, T.E., Washabaugh, K.F., Snowdon, C.T. 2004. Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*. 45(2):84-92.

Appendix 1: Plant families consumed by *Eulemur rubriventer* by site

Family	Site
Acanthaceae	Tala,Vato
Anacardiaceae	Tala,Vato
Anacardiaceae or Elaeocarpaceae	Tala,Vato[1]
Annonaceae	Vato
Apocynaceae	Tala,Vato
Aquifoliaceae	Vato
Araliaceae	Vato
Arecaceae	Tala,Vato
Asteraceae	Vato
Burseraceae	Vato
Cannelaceae	Tala,Vato
Clusiaceae	Tala,Vato
Combretaceae	Vato
Compositae	Tala
Connaraceae	Vato
Cucurbitaceae	Tala,Vato
Cunoniaceae	Tala
Dichapetalaceae	Tala,Vato
Elaeocarpaceae	Vato[1]
Euphorbiaceae	Tala,Vato
Fabaceae/Leguminosae/Papilionaceae	Tala,Vato
Flacourtiaceae	Tala
Guttiferae	Vato
Icaninaceae	Vato
Lauraceae	Tala,Vato
Lobaniaceae	Vato
Loranthaceae	Tala,Vato
Meliaceae	Tala,Vato
Mendonciaceae	Tala,Vato
Monimiaceae	Tala,Vato
Moraceae	Tala,Vato

[1] One species could not be determined at the family level and was narrowed to two families. This secies is listed separately due to the site differences associated with each of the families.

Family	Site
Myrsinaceae	Tala,Vato
Myrtaceae	Tala,Vato
Ochnaceae	Vato
Oleaceae	Tala,Vato
Pandanaceae	Tala,Vato
Passifloraceae	Tala
Proteaceae	Tala,Vato
Rhamnaceae	Tala,Vato
Rubiaceae	Tala,Vato
Rutaceae	Tala
Sapindaceae	Tala,Vato
Sapotaceae	Tala,Vato
Smilaceae	Tala,Vato
Solanaceae	Vato
Sterculiaceae	Tala,Vato
Tiliaceae	Tala,Vato
Torricelliaceae	Vato
Unknown	Tala,Vato
Verbenaceae	Tala
Vitaceae	Tala,Vato

Appendix 2: Plant species and parts consumed by *Eulemur rubriventer* by site

Genus	Species	Vernacular[1]	Site[2]	Part Tala[3]	Part Vato[3]
Agelea	*pentagyna*	Vahimainty	V		RF
Albizia	*chinensis* (Osbeck) Merr.	Albizia	V		RF
Allophylus	*cobbe*	Dikana	T, V	RF, ML	RF
Ambavia	*capuronii* (Cavaco and Keraudren) Le Thomas	Ramiavotoloho	V		RF
Anthocleista	*amplexicaulis*	Dendemy	V		RF
Aphloia	*theaeformis*	Fandramanana	T	RF, UF	
Apodytes	*sp. "*malanimanta"	Malanimanta	V		RF
Bailschmiedia	*oppositifolia*	Sary	T, V	RF, UF	RF, UF, NL
Bailschmiedia	*oppositifolia*	Sary fotsy	T	RF	
Bakerella	*sp. "*tongolahy"	Tongolahy	T, V	RF, NL, FLBL	RF, UF
Beguea	*apetala*	Lanary	T	RF	
Cabucala	*cryptophlebia*	Kaboka	T,V	RF	RF
Campylospermum	*obtusifolium*	Hazombato	V		RF
Canarium	*madagascariense* Engler	Ramy	V		RF, UF
Canthium	*micrantha* Baker	Fatsikahitra	T, V	RF, UF	RF, UF, NL
Canthium	*"fatsikahitra gf"*	Fatsikahitra gf	T, V	RF, UF	RF
Canthium	*"fatsikahitra pf"*	Fatsikahitra pf	V		RF
Carissa	*edulis*	Fatsy	V		RF
Chrysophyllum	*boivinianum (*Pierre) Baehni	Rahiaka	T, V	RF, UF	RF, UF
Cinnamosma	*madagascariensis*	Fanalamangidy	T, V	RF	RF
Cissus	*sp.* "vahirano"	Vahirano	T, V	RF, UF	RF
Cryptocaria	*acuminata*	Tavolo malady	T	RF	
Cryptocaria	*acuminata*	Tavolo ramy	V		RF
Cryptocaria	*cf. "flavescens"*	Tavolo maintso	T, V	RF	RF, UF
Cryptocaria	*cf. crassifolia* (Baker)	Tavolo zahana	V		RF
Cryptocaria	*sp. "*tavolo"	Tavolo	T, V	RF	RF, UF, FLBL,ML
Cryptocaria	*sp. "*manitra"	Tavolo manitra	T, V	RF	RF

[1]"gf" (grande feuille) and "pf" (petite feuille) refer to leaf size
[2]FLN=flower nectar; FLBL=flower bloom; FLBD=flower bud; SD=seed
[3]RF=ripe fruit; UF=unripe fruit; ML=mature leaves; NL=new leaves

Genus	Species	Vernacular[1]	Site[2]	Part Tala[3]	Part Vato[3]
Cryptocaria	*sp. "*molaliambo"	Tavolo molaliambo	T, V	RF	RF
Cryptocaria	*sp. "*pina"	Tavolo pina	T, V	RF	RF
Cryptocaria	*sp. "*rano"	Tavolo rano	T, V	RF	RF
Danais	*sp.* "vahitamboro"	Vahitamboro	T, V	RF,ML,NL	RF, ML,NL
Decarydendron	*helenae*	Amboralahy	V		ML
Dichapetalum	*sp. "*vahimavo"	Vahimavo	V		ML
Dilobeia	*thouarsii* Roemer & Schultes	Ramandriona	T, V	RF	RF
Dombeya	*cf. pubescens*	Hafidahy	T,V	FLBL	FLBL
Dombeya	*sp. "*hafotra makoroho"	Hafotra makoroho	T,V	FLBL	FLBL
Dypsis/Neodypsis	*nodifera*	Sira hazo	T, V	RF	RF
Dypsis/Neodypsis	*sp. "*sira"	Sira	T,V	RF, UF	RF
Embelia	*sp. "*kalamasina"	Kalamasina	V		RF, ML
Enterospermum	*berieranium*	Maranitratoraka	T, V	NL	NL
Eugenia	*jambosa*	Zamborizano	T	FLBD, NL	
Eugenia	*sp.* "andriambolamena"	Andriambolamena	T	RF	
Eugenia	*sp. 1*	Rotra fotsy pf	V		RF
Ficus	*botryoides* (Baker) / *torrentium*	Voara rano	T, V	RF, ML,NL	RF, NL
Ficus	*lutea*	Amotana	T	RF	
Ficus	*pachyclada*	Apana	T, V	RF, UF, NL	RF, UF,NL
Ficus	*pyrifolia*	Nonoka	T, V	RF, UF	RF,UF
Ficus	*sorocoides* or *politoria*	Famakilela	T, V	UF, NL	RF, UF
Ficus	*sp. "*voara"	Voara	T, V	RF, UF, NL	RF
Ficus	*tiliifolia*	Voara be	T	RF, UF	
Ficus	*tiliifolia*	Voara tenany	T	RF, UF	
Gaertnera	*sp. "*bararata"	Bararata	T, V	RF	RF
Gaertnera	*sp. "*bararata gf"	Bararata gf	T	RF, UF	
Gaertnera	*sp. "*hazotoho"	Hazotoho	T	UF	
Garcinia	*tsaratananae*	Kimbaletaka	V		RF
Gouania	*sp. "*vahimpisorona"	Vahimpisorona	T, V	RF	RF
Grewia	*sp. "*hafipotsy"	Hafipotsy	T, V	RF	RF, YL

[1]"gf" (grande feuille) and "pf" (petite feuille) refer to leaf size
[2]FLN=flower nectar; FLBL=flower bloom; FLBD=flower bud; SD=seed
[3]RF=ripe fruit; UF=unripe fruit; ML=mature leaves; NL=new leaves

Genus	Species	Vernacular[1]	Site[2]	Part Tala[3]	Part Vato[3]
Grewia	*sp. "*hafotrataikalalao"	Hafotrataikalalao	T	RF	
Harungana	*madagascariensis* Lam. Ex Poiret	Harongana	V		RF
Ilex	*mitis* (L.) Radilk.	Hazodrano	V		RF
Landolphia	*sp. "*vahiherotra"	Vahiherotra	T	RF,ML, NL	
Landolphia	*sp. "*voatakaboka"	Voatakaboka	T, V	UF	RF
Malleastrum	*sp.* "tongombivy"	Tongombivy	T, V	RF	RF
Mammea	*angustifolia* var. *pseudoprotorhus*	Nato voraka	T, V	RF	RF
Mammea	*vatoensis*	Natojabo	V		FLBL, FLBD,RF
Mascarenhasia	*arborescens*	Herodrano	T	FLN,FLBL	
Melanophylla	*alnifolia* (Baker)	Hazomborondreo	V		RF
Melanophylla	*crenata* (Baker)	Vavaporetaka	V		RF
Mendoncia	*couvanii/avani*	Vahivoraka	T, V	RF	RF, FLBL
Micronychia	*macrophylla* H. Perrier or *madagascariensis*	Sehana	T, V	RF	RF, UF
Micronychia	*sp. "*sandramy fotsy"	Sandramy fotsy	V		RF
Mikania	*scaudens*	Vahivahia	T	ML	
Mussaenda	*erectiloba*	Fatora	T, V	RF, UF	RF, UF
Mussaenda	*lanciolata*	Anambahy	T	RF	
Mussaenda	*lanciolata*	Anambahy	T	RF	
Neotina	*coursii*	Lanary madinka	T, V	RF, UF, SD	RF, UF, SD
Noronhia	*sp. "*solaitra"	Solaitra	T, V	RF, UF	RF
Noronhia	*sp. "*solaitra pf"	Solaitra pf	T	RF	
Noronhia	*sp.* "solaitra fotsy pf"	Solaitra fotsy pf	T, R	RF	RF
Noronhia	*sp. "bavetiravina"*	Solaitra bavetiravina	V		RF
Nuxia	*sp. "*lambinanala"	Lambinanala	V		RF
Nuxia	*verticillata*	Lambinana	T	RF	
Ocotea	*macrocarpa* Kostermans 1939	Vandrika	T	RF	

[1]"gf" (grande feuille) and "pf" (petite feuille) refer to leaf size
[2]FLN=flower nectar; FLBL=flower bloom; FLBD=flower bud; SD=seed
[3]RF=ripe fruit; UF=unripe fruit; ML=mature leaves; NL=new leaves

Genus	Species	Vernacular[1]	Site[2]	Part Tala[3]	Part Vato[3]
Ocotea	*sp. "*varongy"	Varongy	T	RF	
Oncostemon	*botryoides* Baker	Kalafana	T	RF, ML, NL	
Oncostemon	*botryoides* Baker	Kalafana speciale	T, V	RF, UF, ML, NL, FLBD	RF, UF, FLBD, ML, NL
Oncostemon	*sp. "*kalafambakaka"	Kalafambakaka	T, V	RF, ML, NL	ML, NL, FLBD, RF, UF
Oncostemon	*sp. "*kalafambakaka gf"	Kalafambakaka gf	T, V	UF, ML, NL	RF, ML, NL
Oncostemon	*sp. "*kalafambakaka pf"	Kalafambakaka pf	T, V	ML, NL	RF/ML, NL
Pandanus	*sp. "*tsirika"	Tsirika	T, V	RF	RF
Pandanus	*sp.* "vakoana"	Vakoana	T, V	RF,FLBD, FLBL	FLBL
Pauridiantha	*sp.* "vatoana"	Vatoana	V		RF
Potameia	*chartacea*	Sary	T, V	RF, UF	RF,UF,NL
Potameia	*chartacea*	Sary fotsy	T	RF	
Potameia	*crassifolia* Kostermans 1939	Vandrika	T	RF	
Premna	*corymbosa*	Odimamo	T	RF	
Psidium	*guajava*	goavy	T	RF, UF	
Psychotria	*sp.* "fohaninasity"	Fohaninasity	T	RF	
Rhapidiocystis	*brachypoda*	Vahimbarongy	T, V	ML	ML, NL
Rheedia	*aphanophlebia*	Voamalambotaho	T, V	RF	RF, UF
Ruellia	*sp. "*velatra speciale"	Velatra speciale	T, V	ML, NL	ML, NL
Schefflera	*mirianta*	Maroratsana	V		FLBD, FLBL
Schismatoclada	*farhimpensis*	Vavaporetaka	T	RF	
Scolopia	*sp. "*faritraty"	Faritraty	T	RF	
Sideroxylon	*sp. 2*	Nato speciale	V		RF
Sloanea	*rhodantha var. rhodantha* (Baker) Capuron	Vanana	V		RF
Smilax	*sp. "*roindambo"	Roindambo	T, V	RF, UF, NL (buds?)	RF

[1]"gf" (grande feuille) and "pf" (petite feuille) refer to leaf size
[2]FLN=flower nectar; FLBL=flower bloom; FLBD=flower bud; SD=seed
[3]RF=ripe fruit; UF=unripe fruit; ML=mature leaves; NL=new leaves

Genus	Species	Vernacular[1]	Site[2]	Part Tala[3]	Part Vato[3]
Strongylodon	*craveniae*	Vahimberana	T, V	FLN, FLBL, NL	FLN, FLBL
Symphonia	*sp. "*kimba speciale"	Kimba speciale	V		NL
Symphonia	*sp. "*voasavara"	Voasavara	V		UF
Symphonia	*urophylla*	Voatsititinjaza	T	RF	
Syzygium	*emirnensis*	Robary	T, V	RF	RF
Syzygium	*sp. "*rotra"	Rotra	T, V	RF	RF
Syzygium	*sp. "*rotra pf"	Rotra pf	T	RF	
Syzygium	*sp.* "rotra fotsy"	Rotra fotsy	T	RF	
Syzygium	*sp. "*rotra mena"	Rotra mena	T, V	RF	RF
Tambourissa	*thouvenotii*	Ambora pf	T, V	ML	ML
Tambourissa	*trichophylla thouvenotii*	Disohatsaka	T	RF	
Terminalia	*tetranora*	Veso	V		ML,NL
Treculia	*africana*	Apaliala	V		RF, NL
Vepris	*sp.*"apodisosona"	Apodisosona	T	RF	
Vernonia	*sp. 2*	Tavilona	V		NL
Weinmannia	*sp.*"maka"	Maka	T	FLBL	
	spec. indet. "Fanorafa"	Fanorafa	T, V	RF	RF
	spec. indet. "Kilelaka"	Kilelaka	T	ML	
	spec. indet. "Longitra"	Longitra	V		RF
	spec. indet. "Mahanoro"	Mahanoro	T	RF	
	spec. indet. "Nonobary"	Nonobary	T	RF	
	spec. indet. "Sandramy"	Sandramy	T, V	RF	RF
	spec. indet. "Tsimatahodakoto"	Tsimatahodakoto	T, V		RF, UF
	spec. indet. "Vahikisorana"	Vahikisorona	T, V	RF	RF
	spec. indet. "Vahipisorana"	Vahipisorana	T	RF	
	spec. indet. "Voantsosoka	Voantsosoka	V		RF
	spec. indet. "Voasosoka"	Voasosoka	V		RF
	spec. indet. "Voatsirivodrivotra"	Voatsirivodrivotra	V		RF
	spec. indet. "Voatsitity"	Voatsitity	T	RF	

[1]"gf" (grande feuille) and "pf" (petite feuille) refer to leaf size
[2]FLN=flower nectar; FLBL=flower bloom; FLBD=flower bud; SD=seed
[3]RF=ripe fruit; UF=unripe fruit; ML=mature leaves; NL=new leaves

Appendix 3: Group membership and demography of *Eulemur rubriventer* in Vatoharanana and Talatakely

ID	Group/ Alter-nate Group Name	Site	Sex	Age Category at Start of Study	Date of Birth	Year of Birth	Date of Death	Date of Immigration	Date of Departure from Group (possible emigration)	Notes
BR	3	Tala	M	Adult	Unknown	Unknown	N/A	N/A	N/A	Black Red, though collar is Black Purple; Black Red was originally BR's female pairmate, but disappeared. Collared by Toni Lyn Morelli prior to study.
BR (F)	3	Tala	F	Adult	Unknown	Unknown	N/A	N/A	10/6/2003	True Black Red collar; collared by Toni Lyn Morelli prior to study.
Fatty	3	Tala	F	Adult	Unknown	Unknown	N/A	10/22/2003	N/A	No collar

ID	Group/ Alter-nate Group Name	Site	Sex	Age Category at Start of Study	Date of Birth	Year of Birth	Date of Death	Date of Immigration	Date of Departure from Group (possible emigration)	Notes
Infant Fatty	3	Tala	?	N/A	8/25/2004	2004	N/A	N/A	N/A	No collar; very small when first seen on 8/25/04, probably born that week. Not seen with group in 2007.
PY	5/C	Tala	M	Adult	Unknown	Unknown	N/A	N/A	N/A	Pink Yellow
GS	5/C	Tala	F	Adult	Unknown	Unknown	2/27/2004	N/A	N/A	Green Silver; seen vomiting prior to death.
JFGS	5/C	Tala	F	Juvenile	Unknown	2002	N/A	N/A	3/25/2004	No collar; left adult male after mother's death; last seen March 2005 alone near Place de Nocturne.

ID	Group/ Alter-nate Group Name	Site	Sex	Age Category at Start of Study	Date of Birth	Year of Birth	Date of Death	Date of Immigration	Date of Departure from Group (possible emigration)	Notes
InfantGS	5/C	Tala	?	N/A	1/27/2004	2004	N/A	N/A	N/A	No collar; possibly 3 days old when first seen on 1/27/04; death occurred shortly after death of mother.
FNC	5/C	Tala	F	Adult		Unknown	N/A	4/1/2004	N/A	No collar; PY's pairmate following the death of GS.
Infant FNC	5/C	Tala	?	N/A	9/14/2004	2004	N/A	N/A	N/A	No collar
TRI	4/A	Tala	F	Adult	Unknown	Before 1988	N/A	N/A	N/A	Triangle; First captured and collared as an adult by TELO Albert and A. Merenlender c. 1989. Current collar (beginning 2004) is a blue fire hydrant.

ID	Group/ Alter-nate Group Name	Site	Sex	Age Category at Start of Study	Date of Birth	Year of Birth	Date of Death	Date of Immigration	Date of Departure from Group (possible emigration)	Notes
GG	4/A	Tala	M	Adult	Unknown	Unknown	N/A	N/A	N/A	Green Green
BY	4/A	Tala	M	Young Adult	Unknown	est. 2001	N/A	N/A	N/A	Blue Yellow (TRI's offspring)
JT	4/A	Tala	F	Juvenile	Unknown	2002	N/A	N/A	N/A	No collar
InfantTRI1	4/A	Tala	?	N/A	3/23/2004	2004	N/A	N/A	N/A	Extremely small at birth.
InfantTRI2	4/A	Tala	?	N/A	11/2/2004	2004	1/11/2005	N/A	N/A	Extremely small at birth; no longer with group on 1/11/05.
RR	1	Vato	F	Adult	Unknown	Unknown	N/A	N/A	N/A	Radio red; No tag, but radio collar was colored red; Ear notches indicate this individual is "Clara" from Overdorff 1991.
BO	1	Vato	M	Adult	Unknown	Unknown	N/A	N/A	N/A	Blue Orange
JFRR	1	Vato	F	Juvenile	Unknown	2002	N/A	N/A	1/12/2005	No collar; Last seen 1/10/05
JMRR	1	Vato	M	Juvenile	Unknown	est. 2001	N/A	N/A	N/A	No collar

ID	Group/ Alter-nate Group Name	Site	Sex	Age Category at Start of Study	Date of Birth	Year of Birth	Date of Death	Date of Immigration	Date of Departure from Group (possible emigration)	Notes
InfantRR	1	Vato	?	N/A	9/7/2004	2004	N/A	N/A	N/A	No collar
Radio	2	Vato	F	Adult	Unknown	Unknown	N/A	N/A	N/A	No tag, only radio collar
JR	2	Vato	F	Juvenile	Unknown	2002	N/A	N/A	N/A	No collar
PO	2	Vato	M	Adult	Unknown	Unknown	N/A	N/A	N/A	Purple Orange
InfantRadio	2	Vato	?	N/A	8/31/2004	2004	N/A	N/A	N/A	Likely a few days old when observed on 8/31/04.

References

Abbott, D.H., Keverne, E.B., Bercovitch, F.B., Shively, C.A., Mendoza, S.P., Saltzman, W., Snowdon, C.T., Ziegler, T.E., Beanjevic, M., Garland Jr., T., Sapolsky, R.M. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*. 43:67-82.

Abbott, D.H., Saltzman, W., Schultz-Darken, N.J., Tannenbaum, P.L. 1998. Adaptations to subordinate status in female marmoset monkeys. *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology*. 119(3):261-274.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: B.N. Petrov and F. Caski, editors. *Proceedings of the Second International Symposium on Information Theory*. Akademiai Kiado, Budapest. Pp. 267–281.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*. 49:227-267.

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.

Altmann, J. and Muruthi, P. 1988. Differences in daily life between semi-provisioned and wild feeding baboons. *American Journal of Primatology*. 15:213-221.

Altmann, S.A., Post, D.G., Klein, D.F. 1987. Nutrients and toxins of plants in Amboseli, Kenya. *African Journal of Ecology*. 25:279-293.

Amirat, Z., Khammar, F., Brudieux, R. 1980. Seasonal changes in plasma and adrenal concentrations of cortisol, corticosterone, aldosterone, and electrolytes in the adult male sand rat (*Psammomys obesus*). *General and Comparative Endocrinology*. 40(1):36-43.

Arnold, W. and Dittami, J. 1997. Reproductive suppression in male alpine marmots. *Animal Behaviour*. 53(1):53-66.

Arrigo-Nelson, S.J. 2006. *The Impact of Habitat Disturbance on the Feeding Ecology of the Milne-Edwards' Sifaka* (Propithecus edwardsi) *in Ranomafana National Park* [Doctoral Dissertation]. Stony Brook, NY: Stony Brook University. 181 p.

Aschoff, J. 1964. Survival value of diurnal rhythms. In: O.G. Edholm, editor; *Biology of survival*, London. Symposium of the Zoological Society of London, 13: Pp. 79–98.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scandinavica*. 23:355–365.

Astheimer, L.B., Buttemer, W.A., Wingfield, J.C. 1995. Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior*. 29:442-457.

Atsalis, S. 1998. *Seasonal Patterns in Diet, Distribution and Reproduction of* Microcebus rufus *in the Rain Forest of Madagascar* [Doctoral Dissertation]. New York: City University of New York.

Atsalis, S. 1999a. Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 20(2):193-229.

Atsalis S. 1999b. Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *International Journal of Primatology*. 20:883-910.

Bales, K.L., French, J.A., Hostetler, C.M., Dietz, J.M. 2005. Social and reproductive factors affecting cortisol levels in wild female Golden Lion Tamarins *(Leontopithecus rosalia)*. *American Journal of Primatology*. 67:25–35.

Balko, E.A. 1998. *A Behaviorally Plastic Response to Forest Composition and Logging Disturbance by* Varecia variegata variegata *in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Syracuse, NY: SUNY-CESF. 245 p.

Balko, E.A. and Underwood, H.B. 2005. Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*. 66(1):45-70.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W., Simpson, A.J. 1992. Habitat use and resource availability in baboons. *Animal Behaviour*. 43:831-844.

Bawa, K.S. and Hadley, M. 1990. *Reproductive Ecology of Tropical Forest Plants*. Carnforth: Parthenon.

Bearder, S.K., Nekaris, K.A.I., Curtis, D.J. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatologica*. 77:50-71.

Begon, M., Harper, J.L., Townsend, C.R. 1990. *Ecology: Individuals, Populations and Communities, 2nd edition*. Brookline, MA: Blackwell Scientific.

Bercovitch, F.B. 1992. Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior*. 26:272-282.

Bercovitch, F.B. and Ziegler, T.E. 2002. Current topics in primate socioendocrinology. *Annual Review in Anthropology*. 31:45-67.

Berenbaum, M.R. 2007. *Colony Collapse Disorder and Pollinator Decline*. Statement Before the Subcommittee on Horticulture and Organic Agriculture, U.S. House of Representatives.

Berger, P.J., Negus, N.C., Sanders, E.H., Gardner, P.D. 1981. Chemical triggering of reproduction in *Microtus montanus*. *Science*. 214(4516):69-70.

Berry, R.J. and Bronson, F.H. 1992. Life-history and bioeconomy of the house mouse. *Biological Reviews of the Cambridge Philosophical Society*. 67(4):519-550.

Bicca-Marques, J.C., Calegaro-Marques, C. 1998. Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology*. 106(4):533-546.

Bicca-Marques, J.C. 2003. How do howler monkeys cope with habitat fragmentation? In: L.K. Marsh, editor. *Primates in Fragments: Ecology and Conservation*. New York: Kluwer. Pp. 283-303.

Bicca-Marques, J.C. and Calegaro-Marques, C. 1994. Activity budget and diet of *Alouatta caraya*: An age-sex analysis. *Folia Primatologica*. 63(4):216-220.

Birkinshaw, C.R. and Colquhoun, I.C. 1998. Pollination of *Ravenala madagascariensis* and *Parkia madagascariensis* by *Eulemur macaco* in Madagascar. *Folia Primatologica*. 69(5):252-259.

Blanco, M. *In Press*. Reproductive schedules of brown mouse lemurs *(Microcebus rufus)* at Ranomafana National Park, Madagascar. *International Journal of Primatology*.

Boinski, S. 1987. Habitat use by squirrel monkeys in a tropical lowland forest. *Folia Primatologica*. 49:151-167.

Boinski, S., Ehmke, E., Kauffman, L., Schet, S., Vreedzaam, A. 2005. Dispersal patterns among three species of squirrel monkeys *(Saimiri oerstedii, S. boliviensis* and *S. sciureus)*: II. Within-species and local variation. *Behaviour*. 142:633-677.

Bollen, A. and Donati, G. 2005. Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*. 37(1):32-43.

Breuner, C.W., Wingfield, J.C., Romero, L.M. 1999. Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *Journal of Experimental Zoology*. 284(3):334-342.

Bribiescas, R.G. 2001. Reproductive ecology and life history of the human male. *Yearbook of Physical Anthropology*. 44:148-176.

Britt, A. 2000. Diet and feeding behaviour of the black-and-white ruffed lemur *(Varecia variegata variegata)* in the Betampona Reserve, eastern Madagascar. *Folia Primatologica*. 71(3):133-141.

Brockman, D.K. 1994. *Reproduction and mating system of Verreaux's sifaka, Propithecus verreauxi, at Beza Mahafaly, Madagascar*. New Haven, CT: Yale University.

Brockman, D.K., Meltz, K., Whitten, P.L. 2003. Noninvasive assessments of stress in male sifaka *(Propithecus verreauxi)*. *American Journal of Physical Anthropology*. S36:72.

Brockman, D.K. and van Schaik, C.P. 2005. Seasonality and reproductive function. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge University Press. Pp. 269-305.

Brockman, D.K. and Whitten, P.L. 1996. Reproduction in free-ranging *Propithecus verreauxi:* estrus and the relationship between multiple partner matings and fertilization. *American Journal of Physical Anthropology*. 100:57-69.

Brockman, D.K., Whitten, P.L., Richard, A.F. 2000. Birth season cortisol levels in dispersing male *Propithecus verreauxi*. *American Journal of Physical Anthropology*. S30:112-113.

Brockman, D.K., Whitten, P.L., Richard, A.F., Schneider, A. 1998. Reproduction in free-ranging male *Propithecus verreauxi*: Hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*. 105:137-151.

Bronson, F.H. 1989. *Mammalian Reproductive Biology*. Chicago: University of Chicago Press.

Bronson, F.H. 1995. Seasonal variation in human reproduction: Environmental factors. *The Quarterly Review of Biology*. 70(2):141-164.

Bronson, F.H. 1999. Puberty and energy reserves: a walk on the wild side. In: K. Wallen and J. E. Schneider, editors. *Reproduction in Context*. Cambridge: MIT Press. Pp. 15-34.

Bronson, F.H. and Heideman, P.D. 1994. Seasonal regulation of reproduction in mammals. In: E. Knobil and J. D. Neil, editors. *The Physiology of Reproduction, 2nd ed*. New York: Raven Press.

Brown, K.A. and Gurevitch, J. 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences*. 101(16):6045-6049.

Brugiere, D., Gautier, J.P., Moungazi, A., Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest Gabon. *International Journal of Primatology*. 23(5):999-1024.

Brugiere, D., Gautier, J.P., Moungazi, A., Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *International Journal of Primatology*. 23(5):999-1024.

Buck, C.L., O'Reilly, K.M., Kildaw, S.D. 2007. Interannual variability of Black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *General and Comparative Endocrinology*. 150(3):430-436.

Budnitz, N. and Dainis, K. 1975. *Lemur catta*: Ecology and Behavior. In: I. Tattersalll and R. W. Sussman, editors. *Lemur biology*. New York: Plenum. Pp. 219–236.

Burrows, R., Hofer, H., East, M.L. 1994. Demography, extinction and intervention in a small population: The case of the Serengeti wild dogs. *Proceedings of the Royal Society of London Series B*. 256:281-292.

Cade, B.S. 1997. Comparison of tree basal area and canopy cover in habitat models: Subalpine forest. *The Journal of Wildlife Management*. 61(2):326-335.

Cameron, J.L. 1997. Stress and behaviorally induced reproductive dysfunction in primates. *Seminars in Reproductive Endocrinology*. 15(1):37-45.

Cant, J.G.H., Youlatos, D., Rose, M.D. 2001. Locomotor behavior of *Lagothrix lagtricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. *Journal of Human Evolution*. 41:141-166.

Carlstead, K., Brown, J.L., Monfort, S.L., Killens, R., Wildt, D.E. 1992. Urinary monitoring of adrenal responses to psychological stressors in domestic and nondomestic felids. *Zoo Biology*. 11(3):165-176.

Carlstead, K. and Brown, J.L. 2005. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black *(Diceros bicornis)* and white *(Ceratotherium simum)* rhinoceros. *Zoo Biology*. 24(3):215-232.

Carrillo, E., Saenz, J.C., Fuller, T.K. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. *Biological Conservation*. 108(3):317-324.

Carthew, S.M. and Goldingay, R.L. 1997. Non-flying mammals as pollinators. *Trends in Ecology and Evolution*. 12(3):104-108.

Cavigelli, S.A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*. 57(4):935-944.

Cavigelli, S.A., Dubovick, T., Levash, W., Jolly, A., Pitts, A. 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs *(Lemur catta)*. *Hormones and Behavior*. 43:166–179.

Cavigelli, S.A., Monfort, S.L., Whitney, T.K., Mechref, Y.S., Novotny, M., McClintock, M.K. 2005. Frequent serial fecal corticoid measures from rats reflect circadian and ovarian corticosterone rhythms. *Journal of Endocrinology*. 184(1):153-163.

Chamove, A.S. and Bowman, R.E. 1978. Rhesus plasma cortisol response at four dominance positions. *Aggressive Behavior*. 4:43-55.

Champoux, M., Zanker, D., Levine, S. 1993. Food search demand effort effects on behavior and cortisol in adult female squirrel monkeys. *Physiology and Behavior*. 54:1091-1097.

Chapman, C. 1988. Patch use and patch depletion by the spider and howling monkeys of Santa-Rosa National Park, Costa Rica. *Behaviour*. 105:99-116.

Chapman, C.A. 1987. Flexible diets of three species of Costa Rican primates. *Folia Primatologica*. 49:90-105.

Chapman, C.A., Chapman, L.J., Wrangham, R., Hunt, K., Gebo, D., Gardner, L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica*. 24:527-531.

Chapman, C.A., Wrangham, R., Chapman, L.J. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*. 26:160-171.

Chapman, C.A. and Chapman, L.J. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*. 40:215-232.

Chapman, C.A., Saj, T.L., Snaith, T.V. 2007. Temporal dynamics of nutrition, parasitism, and stress in Colobus monkeys: Implications for population regulation and conservation. *American Journal of Physical Anthropology*. 134(2):240-250.

Chapman, C.A., Wasserman, M.D., Gillespie, T.R., Speirs, M.L., Lawes, M.L., Saj, T.L., Ziegler, T.E. 2006. Do food availability, parasitism, and stress have synergistic effects on Red Colobus populations living in forest fragments? *American Journal of Physical Anthropology*. 131:525-534.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K., Zanne, A.E. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*. 15:189-211.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K., Zanne, A.E. 2000. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*. 15(02):189-211.

Charnov, E. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.

Charnov, E.L. and Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evolutionary Anthropology*. 1(6):191-194.

Chatterton, R.T., Kazer, R.R., Rebar, R.W. 1991. Depletion of luteal phase serum progesterone during constant infusion of cortisol phosphate in the cynomolgus monkey. *Fertility and Sterility*. 56:547-554.

Chen, X. 2003. Assessing phenology at the biome level. In: M. D. Schwartz, editor. *Phenology: An Integrative Environmental Science*. Dordecht: Kluwer Academic. Pp. 285-300.

Chivers, D.J. 1991. Species differences in tolerance to environmental change. In: H.O. Box, editor. *Primate Responses to Environmental Change*. New York: Chapman and Hall. Pp. 5-37.

Chrousos, G.P. 1998. Stressors, stress, and neuroendocrine integration of the adaptive response: The 1997 Hans Selye Memorial Lecture. *Annals of the New York Academy of Sciences*. 851(1):311-335.

Chrousos, G.P., Torpy, D.J., Gold, P.W. 1998. Interactions between the hypothalamic-pituitary-adrenal axis and the female reproductive system: Clinical implications. *Annals of Internal Medicine*. 129:229-240.

Clarke, M.R., Harrison, R.M., Didier, E.S. 1996. Behavioral, immunological, and hormonal responses associated with social change in rhesus monkeys *(Macaca mulatta)*. *American Journal of Primatology*. 39:223-233.

Clutton-Brock, T.H., Harvey, P.H. 1977. *Primate Ecology*. T.H. Clutton-Brock, editor. London: Academic Press.

Clutton-Brock, T.H., Harvey, P.H., Rudder, B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*. 269:797-800.

Cockrem, J.F. 2005. Conservation and behavioral neuroendocrinology. *Hormones and Behavior*. 48(4):492-501.

Coe, C.L., Franklin, D., Smit, E.R., Levine, S. 1982. Hormonal responses accompanying fear and agitation in the squirrel monkey. *Physiology and Behavior*. 29:1051-1057.

Coe, C.L. and Levine, S. 1995. Diurnal and annual variation of adrenocortical activity in the squirrel monkey. *American Journal of Primatology*. 35:283-292.

Coe, C.L. and Scheffler, J. 1989. Utility of immune measures for evaluating psychological well-being in nonhuman primates. *Zoo Biology*. 1:89-99.

Coe, M.J. and Isaac, F.M. 1965. Pollination of the baobab *(Adansonia digitata* L.) by the lesser bush baby *(Galago crasicaudatus* E. Geoffroy). *East African Wildlife Journal*. 3(123-124).

Coelho, A.M. 1986. Time and energy budgets. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology*. New York: Alan R. Liss. Pp. 141–166.

Cohen, S. 1988. Psychosocial models of the role of social support in the etiology of physical disease. *Health Psychology*. 7:269-297.

Colquhoun, I.C. 1998. Cathemeral behavior of *Eulemur macaco macaco* at Ambato Massif, Madagascar. *Folia Primatologica*. 69(Suppl 1):22-34.

Colquhoun, I.C. 2006. Predation and cathemerality: Comparing the impact of predators on the activity patterns of Lemurids and Ceboids. *Folia Primatologica*. 77:143-165.

Colwell, M.A., Gratto, C.L., Oring, L.W., Fivizzani, A.J. 1988. Effects of blood sampling on shorebirds: Injuries, return rates and clutch desertions. *Condor*. 90:942-945.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a non-equilibrium state. *Science*. 199(4335):1302-1310.

Cook, C.J., Mellor, D.J., Harris, P.J., Ingram, J.R., Matthews, L.R. 2000. Hands-on and hands-off measurement of stress. In: G.P. Moberg and J.A. Mench, editors. *The Biology of Animal Stress*. New York: CABI Publishing. Pp. 123–146.

Coop, R.L. and Holmes, P.H. 1996. Nutrition and parasite interaction. *International Journal of Parasitology*. 26:951-962.

Cotter, R.C. and Gratto, C.J. 1995. Effects of nest and brood visits and radio transmitters on rock ptarmigan. *Journal of Wildlife Management*. 59:93-98.

Creel, S., Creel, N.M., Monfort, S.L. 1997. Radiocollaring and stress hormones in African wild dogs. *Conservation Biology*. 11:544-548.

Cross, N. and Rogers, L.J. 2004. Diurnal cycle in salivary cortisol levels in common marmosets. *Developmental Psychobiology*. 45(3):134-139.

Curtis, D., Zaramody, A, Martin, RD. 1999. Cathemerality in the Mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology*. 47:279–298.

Curtis, D.J. 2004. Diet and nutrition in wild mongoose lemurs *(Eulemur mongoz)* and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology*. 124(3):234-247.

Curtis, D.J. and Rasmussen, M.A. 2002. Cathemerality in lemurs. *Evolutionary Anthropology*. S1:83-86.

Curtis, D.J. and Rasmussen, M.A. 2006. The evolution of cathemerality in primates and other mammals: A comparative and chronoecological approach. *Folia Primatologica*. 77(1-2):178-193.

Curtis, D.J., Zaramody, A., Martin, R.D. 1999. Cathemerality in the mongoose lemur, *Eulemur mongoz*. *American Journal of Primatology*. 47(4):279-298.

Cuthill, I.C. and Houston, A.I. 1997. Managing time and energy. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach*. Massachusetts: Blackwell Science. Pp. 97-120.

Cyr, N.E. and Michael Romero, L. 2007. Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *General and Comparative Endocrinology*. 151(1):82-89.

Czekala, N.M., Lance, V.A., Sutherland-Smith, M. 1984. Diurnal urinary corticoid excretion in the human and gorilla. *American Journal of Primatology*. 34:29-34.

da Silva Mota, M.T., Franci, C.R., de Sousa, M.B.C. 2006. Hormonal changes related to paternal and alloparental care in common marmosets *(Callithrix jacchus)*. *Hormones and Behavior*. 49:293-302.

Daan, S. and Tinbergen, J.M. 1997. Adaptation to Life Histories. In: J.R. Krebs and N.B. Davies, editors. *Behavioural Ecology: An Evolutionary Approach, Fourth Edition*. Oxford: Blackwell Science. Pp. 311-333.

DaGosto, M. 1989. Locomotion of *Propithecus diadema* and *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 78:209.

Dagosto, M. and Yamashita, N. 1998. Effect of habitat structure on positional behavior and support use in three species of lemur. *Primates*. 39(4):459-472.

Dallman, M. 2003. Stress by any other name…? *Hormones and Behavior*. 43(1):18-20.

Dallman, M.F. 1993. Stress update: Adaptation of the hypothalamic-pituitary-adrenal axis to chronic stress. *Trends in Endocrinology and Metabolism*. 4(2):62-69.

Dallman, M.F., Strack, A.M., Akana, S.F., Bradbury, M.J., Hanson, E.S., Scribner, K.A., Smith, M. 1993. Feast and famine: Critical role of glucocorticoids with insulin in daily energy-flow. *Frontiers in Neuroendocrinology*. 14(4):303-347.

Dasilva, G.L. 1992. The western black-and-white colobus as a low-energy strategist: Activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology*. 61(1):79-91.

Dausmann, K., Glos, J., Ganzhorn, J.U., Heldmaier, G. . 2004. Hibernation in a tropical primate. *Nature*. 429:825-826.

Dausmann, K., Glos, J., Ganzhorn, J.U., Heldmaier, G. 2004. Hibernation in a tropical primate. *Nature*. 429:825-826.

de Pedro, N., Delgado, M.J., Pinillos, M.L., Alonso-Gomez, A.L., Alonso-Bedate, M. 1998. Daily rhythms in NAT activity, cortisol, glucose, glycogen and catecholamines in tench (*Tinca tinca*). *Polskie Archiwum Hydrobiologii* 45(3):321-329.

Defler, T.R. 1995. The time budget of a group of wild woolly monkeys *(Lagothrix lagotricha)*. *International Journal of Primatology*. 16(1):107-120.

DeJong, T.M. 1975. A comparison of three diversity indices based on their components of richness and evenness. *Oikos*. 26(2):222-227.

Dettmer, E.L., Phillips, K.A., Rager, D.R., Bernstein, I.S., Fragaszy, D.M. 1996. Behavioral and cortisol responses to repeated capture and venipuncture in *Cebus apella*. *American Journal of Primatology*. 38(4):357-362.

Dew, J.L. and Wright, P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica*. 30(3):425-437.

Dewar, R.E. and Richard, A.F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences*. 104(34):13723-13727.

Dewar, R.E. and Wallis, J.R. 1999. Geographical patterning of interannual rainfall variability in the tropics and near tropics: An L-moments approach. *Journal of Climate*. 12(12):3457-3466.

DiBitetti, M.S. and Janson, C.H. 2000. When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*. 50:109-130.

DiFiore, A. and Rodman, P.S. 2001. Time allocation patterns of lowland woolly monkeys *(Lagothrix lagotricha poeppigii)* in a neotropical terra firma forest. *International Journal of Primatology*. 22:449–480.

DiFiore, A. and Suarez, S. 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition*. (Advance Online Publication):1-13.

Dobbin, J.P., Marth, M., McCain, G.A., Martin, R.A., Cousin, K. 1991. Cytokine production and lymphocyte transformation during stress. *Brain Behavior and Immunity*. 5:339-348.

Donati, G. and Borgognini-Tarli, S.M. 2006. Influence of abiotic factors on cathemeral activity: The case of Eulemur fulvus collaris in the littoral forest of Madagascar. . *Folia Primatologica*. 77(1-2):104-122.

Donati, G., Lunardini, A., Kappeler, P.M. 1999. Cathemeral activity of red-fronted brown lemurs *(Eulemur fulvus rufus)* in the Kirindy Forest/CFPF. *New Directions in Lemur Studies*. New York: Kluwer Acad/Plenum Press. Pp. 119-137.

Donque, G. 1972. The climatology of Madagascar. In: R. Battistini and G. Richard-Vindard, editors. *Biogeography and Ecology of Madagascar*. The Hague: W. Junk. Pp. 87-144.

Doran, D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology*. 18(2):183-206.

Dorr, L.J. 2003. Identifying Malagasy trees. *Bioscience*. 53(7):678-680.

Drent, R.H. and Daan, S. 1980. The prudent parent - energetic adjustments in avian breeding. *Ardea*. 68(1-4):225-252.

Dufils, J.-M. 2003. Remaining forest ecology. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 88-96.

Dunbar, R.I.M. 1988. *Primate Social Systems*. Ithaca, New York: Cornell University Press.

Dunbar, R.I.M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*. 31(1):35-49.

DuPuy, D.J., Moat, J. 1995. A refined classification of the primary vegetation based on the underlying geology: Using GIS to map its distribution and to assess its conservation status. In: W.R. Laurenco, editor. *Biogeography of Madagascar*. Paris: Unesco. Pp. 205-218.

DuPuy, D.J. and Moat, J. 2003. Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 51-74.

Durham, D.L. 2003. *Variation in Responses to Forest Disturbance and the Risk of Local Extinction: A Comparative Study of Wild* Eulemurs *at Ranomafana National Park, Madagascar* [Doctoral Dissertation]. Davis: University of California, Davis. 170 p.

Ebensperger, L.A., Hurtado, M.J. 2005. Seasonal changes in the time budget of degus, *Octodon degus*. *Behaviour*. 142:91-112.

Eger, J.L., Mitchell, L. 2003. Chiroptera, Bats. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1287-1298.

Ellison, P.T., Valeggia, C.R., Sherry, D.S. 2005. Human birth seasonality. In: D. K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 379-399.

Elsom, E. 2002. *A Preliminary Inventory of the Platynini (Coleoptera: Carabidae) of Ranomafana National Park* [Master's Thesis]. San Francisco: San Francisco State University.

Engqvist, A. and Richard, A.F. 1991. Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatologica*. 57:169-172.

Erkert, H.G. and Cramer, B. 2006. Chronobiological background to cathemerality: Circadian rhythms in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). *Folia Primatologica*. 77(1-2):87-103.

Esch, G.W., Gibbons, J.W., Bourque, J.E. 1975. An analysis of the relationship between stress and parasitism. *American Midland Naturalist*. 93(2):339-353.

Estrada, A. and Coates-Estrada, R. 1985. A preliminary study of resource overlap between howling monkeys (*Alouatta palliata*) and other arboreal mammals in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology* 9:27-37.

Estrada, A., Juan-Solano, S., Ortíz Martínez, T., Coates-Estrada, R. 1999. Feeding and general activity patterns of a howler monkey *(Alouatta palliata)* troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology*. 48(3):167-183.

Fairgrieve, C. and Muhumuza, G. 2003. Feeding ecology and dietary differences between blue monkey *(Cercopithecus mitis stuhlmanni* Matschie) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *African Journal of Ecology*. 41:141-149.

Fernandez-Duque, E., Erkert, H.G. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. *Folia Primatologica*. 77:123–138.

Ferrari, S.F. and Strier, K.B. 1992. Exploitation of *Mabea fistulifera* nectar by marmosets *(Callithrix flaviceps)* and muriquis *(Brachyteles arachnoides)* in south-east Brazil. *Journal of Tropical Ecology*. 8:225-239.

Fichtel, C., Kraus, C., Ganswindt, A., Heistermann, M. 2007. Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas *(Propithecus verreauxi)*. *Hormones and Behavior.* 51(5):640-648.

Fivizzani, A.J., Spieler, R.E., Noeske, T.A. 1984. The influence of ambient temperature on the daily variation of serum cortisol in the Banded Killifish, *Fundulus diaphanus*. *Journal of Interdisciplinary Cycle Research*. 15(1):3-8.

Fleming, A.S., Corter, C., Stallings, J., Steiner, M. 2002. Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*. 42:399-413.

Foley, C.A.H., Papageorge, S., Wasser, S.K. 2001. Noninvasive stress and reproductive measures of social and ecological pressures in free-ranging African elephants. *Conservation Biology*. 15(4):1134-1142.

Fox, E.A., Van Schaik, C.P., Sitompul, A., Wright, D.N. 2004. Intra- and interpopulational differences in orangutan *(Pongo pygmaeus)* activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology*. 125(2):162-174.

French, J.A., Koban, T., Rukstalis, M., Ramirez, S.M., Bardi, M., Brent, L. 2004. Excretion of urinary steroids in pre- and postpartum female baboons. *General and Comparative Endocrinology*. 137(1):69-77.

Fulkerson, W.J. and Tang, B.Y. 1979. Ultradian and circadian rhythms in the plasma concentration of cortisol in sheep. *Journal of Endocrinology*. 81(1):135-141.

Ganzhorn, J.U. 1995a. Cyclones over Madagascar: Fate or fortune? . *Ambio*. 24:124-125.

Ganzhorn, J.U. 2003. Habitat description and phenology. In: J.M. Setchell, Curtis, D.J., editor. *Field and Laboratory Methods in Primatology: A Practical Guide*. Cambridge: Cambridge University Press. Pp. 40-56.

Ganzhorn, J.U. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia*. 91(4):540-547.

Ganzhorn, J.U. 1995b. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*. 76(7):2084-2096.

Ganzhorn, J.U., Langrand, O., Wright, P.C., O'Connor, S., Rakotosamimanana, B., Feistner, A.T.C., Rumpler, Y. 1996/7. The state of lemur conservation in Madagascar. *Primate Conservation*. 17:70-86.

Ganzhorn, J.U., Fietz, J., Rakotovao, E., Schwab, D., Zinner, D. 1999a. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*. 13:794-804.

Ganzhorn, J.U., Malcomber, S., Andrianantoanina, O., Goodman, S.M. 1997. Habitat characteristics and lemur species richness in Madagascar. *Biotropica*. 29(3):331-343.

Ganzhorn, J.U., Wright, P.C., Ratsimbazafy, H.J. 1999b. Primate communities: Madagascar. In: J.G. Fleagle, C.H. Janson and K. Reed, editors. *Primate Communities*. Cambridge: Cambridge University Press. Pp. 75-89.

Ganzhorn, J.U., Goodman, S.M., Dehgan, A. 2003a. Effects of forest fragmentation on small mammals and lemurs. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1228-1234.

Ganzhorn, J.U., Klaus, S., Ortmann, S., Schmid, J. 2003b. Adaptations to seasonality: Some primate and nonprimate examples. *Primate Life Histories and Socioecology*. Chicago: University of Chicago Press. Pp. 132.

Garber, P.A. 1988. Foraging decisions during nectar feeding by tamarin monkeys *(Saguinus mystax* and *Saguinus fuscicollis,* Callitrichidae, Primates) in Amazonian Peru. *Biotropica*. 20:100-106.

Garber, P.A. 1993. Seasonal patterns of diet and range in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology*. 14:145-166.

Gautier-Hion, A., Gautier, J.P., Quiris, R. 1981. Forest structure and food availability as complementary factors influencing the habitat use by a troop of monkeys *(Cercopithecus cephus)*. *Revue d'ecologie*. 35:511-536.

Gautier-Hion, A. and Michaloud, G. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*. 70(6):1826-1833.

Geiser, F., Ruf, T. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology*. 68:935–966.

Gelatt, T.S., Siniff, D.B., Estes, J.A. 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. *Journal of Wildlife Management*. 66(1):29-39.

Glander, K.E. 1981. Feeding patterns in mantled howling monkeys In: A. Kamil and T. Sargent, editors. *Foraging Behavior: Ecological and Psychological Approaches*. New York: Garland Press. Pp. 231-258.

Glander, K.E., Wright, P.C., Daniel, P.S., Merenlender, A.M. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *Journal of Human Evolution*. 22:1-17.

Glander, K.E., Wright, P.C., Daniels, P.S., Merenlender, A.M. 1992. Morphometrics and testicle size in rain forest lemur species from southwestern Madagascar. *Journal of Human Evolution*. 92:1-17.

Glessner, K.D.G. and Britt, A. 2005. Population density and home range size of *Indri indri* in a protected low altitude rain forest. *International Journal of Primatology*. 26(4):855-872.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T. 2004. Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology*. 123:250-276.

Goldsmith, M.L. 1999. Ecological constraints on the foraging effort of western gorillas *(Gorilla gorilla gorilla)* at Bai Hokou, Central African Republic. *International Journal of Primatology*. 20(1):1-23.

Goldstein, S.J. and Richard, A.F. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *International Journal of Primatology*. 10(6):531-567.

Goodman, S.M. and Ganzhorn, J.U. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Review of Ecology*. 52:321-329.

Gorchav, D.L. 1990. Pattern, adaptation, and constraint in fruiting synchrony within vertebrate-dispersed woody plants. *Oikos*. 58(2):169-180.

Gould, L., Sussman, R.W., Sauther, M.L. 1999. Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs *(Lemur catta)* in southwestern Madagascar. *International Journal of Primatology*. 20(1):69-84.

Gould, L., Sussman, R.W., Sauther, M.L. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*. 120(2):182-194.

Gould, L., Ziegler, T.E., Wittwer, D.J. 2005. Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs *(Lemur catta)* at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*. 67(1):5-23.

Goymann, W., East, M.L., Wachter, B., Honer, O.P., Möstl, E., Van't Hof, T.J., Hofer, H. 2001. Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 268(1484):2453-2459.

Goymann, W., Möstl, E., Van't Hof, T., East, M.L., Hofer, H. 1999. Noninvasive fecal monitoring of glucocorticoids in spotted hyenas, *Crocuta crocuta*. *General and Comparative Endocrinology*. 114(3):340-348.

Grassi, C. 1998. Forest composition and bamboo distribution: influences on the distribution of *Hapalemur* species. *American Journal of Physical Anthropology*.

Grassi, C. 2001. *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore* [Doctoral Dissertation]. Austin: University of Texas at Austin.

Green, G.M., Sussman, R.W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*. 248:212-215.

Green, G.M. and Sussman, R.W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science*. 248:212-215.

Gross, T. 1991. Development and use of fecal steroid analyses in captive exotic mammals and birds; *Society for Theriogenology, Proceedings of Annual Meeting*: Pp. 66-74.

Gursky, S. 2000. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*. 21:477-495.

Gust, D.A., Gordon, T.P., Hambright, M.K. 1993. Response to removal from and return to a social group in adult male rhesus monkeys. *Physiology & Behavior*. 53(3):599-602.

Gust, D.A., Gordon, T.P., Wilson, M.E., Brodie, A.R., Ahmed-Ansari, A., McClure, H.M. 1996. Group formation of female pigtail macaques *(Macaca nemestrina)*. *American Journal of Primatology*. 39:263-273.

Gust, D.A., Wilson, M.E., Stocker, T., Conrad, S., Plotsky, P.M., Gordon, T.P. 2000. Activity of the hypothalamic-pituitary-adrenal axis is altered by aging and exposure to social stress in female rhesus monkeys. *Journal of Clinical Endocrinology and Metabolism*. 85(7):2556-2563.

Halle, S. 2006. Polyphasic Activity Patterns in Small Mammals. *Folia Primatologica*. 77(1-2):15-26.

Halle, S. and Stenseth, N.C. 2000. *Activity Patterns of Small Mammals: An Ecological Approach*. Berlin: Springer.

Hammond, K.A. and Diamond, J. 1997. Maximal sustained energy budgets in humans and animals. *Nature*. 386:457-462.

Hanya, G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: Effects of food and temperature. *American Journal of Primatology*. 63:165-177.

Harcourt, A. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: T Caro, editor. *Behavioral Ecology and Conservation Biology*. New York: Oxford University Press. Pp. 56-79.

Harcourt, C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *Journal of Zoology*. 223:667-674.

Harcourt, C. and Thornback, J. 1990. *Lemurs of Madagascar and the Comoros. The IUCN Red Data Book*. Gland, Switzerland: IUCN.

Harlow, H.J., Thorne, E.T., Williams, E.S., Belden, E.L., Gern, W.A. 1987. Cardiac frequency: A potential predictor of blood cortisol levels during acute and chronic stress exposure in Rocky Mountain bighorn sheep *(Ovis canadensis)*. *Canadian Journal of Zoology*. 65:2028-2034.

Harper, J.N. and Austad, S.M. 2002. Fecal glucocorticoids: a noninvasive method of measuring adrenal activity in wild and captive rodents. *Physiological and Biochemical Zoology*. 73:12-22.

Hay, M. and Mormede, P. 1998. Urinary excretion of catecholamines, cortisol and their metabolites in Meishan and Large White sows: validation as a non-invasive and integrative assessment of adrenocortical and sympathoadrenal axis activity. *Veterinary Research*. 29(2):119-128.

Hemingway, C.A. 1995. *Feeding and Reproductive Strategies of* Propithecus diadema edwardsi [Doctoral Dissertation]. Durham: Duke University.

Hemingway, C.A. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edward's sifaka, *Propithecus diadema edwardsi,* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 17:637-657.

Hemingway, C.A. 1998. Selectivity and variability in the diet of Milne-Edwards' sifakas *(Propithecus diadema edwardsi)*: Implications for folivory and seed-eating. *International Journal of Primatology*. 19(2):355-377.

Hemingway, C.A. 1999. Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? *Behavioral Ecology and Sociobiology*. 45:311-322.

Hemingway, C.A. and Bynum, N. 2005. The influence of seasonality on primate diet and ranging. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 57-104.

Hemingway, C.A. and Overdorff, D.J. 1999a. Food for thought: Evaluating phenological methods as food availability estimates. *American Journal of Physical Anthropology*. S28:149.

Hemingway, C.A. and Overdorff, D.J. 1999b. Sampling effects on food availability estimates: Phenological method, sample size, and species composition. *Biotropica*. 31:354-364.

Hendrie, T.A., Peterson, P.E., Short, J.J., Tarantal, A.F., Rothgarn, E., Hendrie, M.I., Hendrickx, A.G. 1996. Frequency of prenatal loss in a macaque breeding colony. *American Journal of Primatology*. 40(1):41-53.

Hennessy, M.B., Mendoza, S.P., Mason, W.A., Moberg, G.P. 1995. Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*. 57(2):331-338.

Hennessy, M.B., Heybach, J.P., Vernikos, J., Levine, S. 1979. Plasma corticosterone concentrations sensitively reflect levels of stimulus intensity in the rat. *Physiology and Behavior*. 22:821-825.

Hennessy, M.B., Mendoza, S.P., Mason, W.A., Moberg, G.P. 1995. Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*. 57(2):331-338.

Hill, R.A. 2005. Day length seasonality and the thermal environment. In: D.K. Brockman and C.P. van Schaik, editors. *Primate Seasonality: Implications for Human Evolution*. Cambridge: Cambridge University Press. Pp. 197-213.

Hill, R.A. 2006. Why be diurnal? Or, why not be cathemeral? *Folia Primatologica*. 77:72-86.

Hladik, A. 1980. The dry forest of the west coast of Madagascar: Climate, phenology, and food available for Prosimians. In: P. Charles Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, A. Schilling and J.J. Petter, editors. *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*. New York: Academic Press. Pp. 3-40.

Hladik, C.M. 1979. Diet and ecology of prosimians. In: G.A. Doyle and R.D. Martin, editors. *The Study of Prosimian Behavior*. London: Academic Press. Pp. 307-358.

Hladik, C.M. and Charles-Dominique, P. 1974. The behaviour and ecology of the sportive lemur *(Lepilemur mustelinus)* in relation to its dietary peculiarities. In: G.A. Doyle, R.D. Martin and A.C. Walker, editors. *Prosimian Biology*. London: Duckworth. Pp. 23-37.

Hofer, H. and East, M.L. 1998. Biological conservation and stress. In: A.P. Møller, M. Milinski and P.J.B. Slate, editors. *Advances in the Study of Behavior, Vol 27*. San Diego: Academic Press. Pp. 405-525.

Homan, R.N., Regosin, J.V., Rodrigues, D.M., Reed, J.M., Windmiller, B.S., Romero, L.M. 2003. Impacts of varying habitat quality on the physiological stress of spotted salamanders *(Ambystoma maculatum)*. *Animal Conservation*. 6(1):11-18.

Honess, P.E. and Marin, C.M. 2006. Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews*. 30(3):390-412.

Hruschka, D.J., Kohrt, B.A., Worthman, C.M. 2005. Estimating between- and within-individual variation in cortisol levels using multilevel models. *Psychoneuroendocrinology*. 30(7):698-714.

Hubbell, S.P. and Foster, R.B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: S.L. Sutton, T.C Whitmore and A.C. Chadwick, editors. *Tropical Rain Forest: Ecology and Management* Oxford: Blackwell Scientific Publications. Pp. 25-41.

Huber, S., Palme, R., Arnold, W. 2003. Effects of season, sex, and sample collection on concentrations of fecal cortisol metabolites in red deer *(Cervus elaphus)*. *General and Comparative Endocrinology*. 130(1):48-54.

Humphries, M.M., Umbanhowar, J., McCann, K.S. 2004. Bioenergetic prediction of climate change impacts on northern mammals 1. *Integrative and Comparative Biology*. 44(2):152-162.

Hwang, M.H. and Garshelis, D.L. 2007. Activity patterns of Asiatic black bears *(Ursus thibetanus)* in the Central Mountains of Taiwan. *Journal of Zoology*. 271(2):203-209.

Irwin, M.T. 2006. *Ecological Impacts of Forest Fragmentation on Diademed Sifakas* (Propithecus diadema) *at Tsinjoarivo, eastern Madagascar: Implications for Conservation in Fragmented Landscapes* [Doctoral Dissertation]. Stony Brook, New York: Stony Brook University. 410 p.

Irwin, M.T. 2007. Living in forest fragments reduces group cohesion in Diademed Sifakas *(Propithecus diadema)* in Eastern Madagascar by reducing food patch size. *American Journal of Primatology*. 69:434-447.

Irwin, M.T., Johnson, S.E., Wright, P.C. 2005. The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx*. 39(2):204-218.

IUCN. 2006. *2006 IUCN Red List of Threatened Species*.

Iwamoto, T. and Dunbar, R.I.M. 1983. Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *The Journal of Animal Ecology*. 52(2):357-366.

Janson, C. and Verdolin, J. 2005. Seasonality of primate births in relation to climate. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. New York: Cambridge Univ Press. Pp. 307-350.

Janson, C.H., Terborgh, J., Emmons, L.H. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica*. 14(1-6).

Johns, A.D. and Skorupa, J.P. 1987. Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*. 8(2):157-191.

Johnson, B.K. 2002. *Soil Characterization and Reconnaissance Survey of the Ranomafana National Park Area, Southeastern Madagascar* [Doctoral Dissertation]. Raleigh, NC: North Carolina State University.

Johnson, R. 2007. *CRS Report for Congress: Recent Honey Bee Colony Declines.* Science Congressional Research Division. Resources, and Industry Division. p 13

Johnson, S.E. 2002. *Ecology and Speciation in Brown Lemurs: White-collared Lemurs* (Eulemur albocollaris) *and Hybrids* (Eulemur albocollaris *X* Eulemur fulvus rufus) *in Southeastern Madagascar* [Doctoral Dissertation]. Austin: University of Texas at Austin. 288 p.

Johnson, S.E. and Overdorff, D.J. 1999. Census of brown lemurs (*Eulemur fulvus spp*.) in southeastern Madagascar: Methods-testing and conservation implications. *American Journal of Primatology*. 47(1):51-60.

Jolly, A. 1966. *Lemur Behavior: A Madagascar Field Study*. Chicago: University of Chicago Press.

Jolly, A. 1984. The puzzle of female feeding priority. In: M. Small, editor. *Female Primates: Studies by Women Primatologists*. New York: Alan R. Liss. Pp. 197-215.

Jolly, A., Dobson, A., Rasamimanana, H.M., Walker, J., O'Connor, S., Solberg, M., Perel, V. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *International Journal of Primatology*. 23(2):327-353.

Jones, J.P.G., Andriahajaina, F.B., Hockley, N.J., Balmford, A., Ravoahangimalala, O.R. 2005. A multidisciplinary approach to assessing the sustainability of freshwater crayfish harvesting in Madagascar. *Conservation Biology*. 19(6):1863-1871.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*. 78(1):57-66.

Jury, M.R. 2003. The climate of Madagascar. In: S.M. Goodman and J.P. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 75-87.

Kaplan, J.R. 1986. Psychological stress and behavior in nonhuman primates. In: G. Mitchell and J. Erwin, editors. *Comparative Primate Biology*. New York: Alan R. Liss.

Kappeler, P.M. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*. 57(3):132-146.

Kappeler, P.M. 1996. Causes and consequences of life-history variation among strepsirhine primates. *American Naturalist*. 148:868-891.

Kappeler, P.M., Erkert, H.G. . 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs *(Eulemur fulvus rufus)*. *Behavioural Ecology and Sociobiology*. 54:359–369.

Keay, J.M., Singh, J., Gaunt, M.C., Kaur, T. 2006. Fecal glucocorticoids and their metabolites as indicators of stress in various mammalian species: A literature review. *Journal of Zoo and Wildlife Medicine*. 37(3):234-244.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, D., Dale, B.W., Stephenson, T.R. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management*. 64:450-462.

Keller, S.E., Weiss, J.M., Schleifer, S.L., Miller, N.E., Stern, M. 1983. Stress-induced suppression of immunity in adrenalectomized rats. *Science*. 221:1301-1304.

Kenagy, G.J., Sharbaugh, S.M., Nagy, K.A. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia*. 78(2):269-282.

Kery, M. and Schmid, H. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology*. 43(1):101-110.

Keuroghlian, A. 2003. *The Response of Peccaries to Seasonal Fluctuations in an Isolated Patch of Tropical Forest* [Doctoral Dissertation]. Reno, Nevada: University of Nevada. 158 p.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems & Environment*. 74(1-3):373-393.

Khansari, D.N., Murgo, A.J., Faith, R.E. 1990. Effects of stress on the immune system. *Immunology Today*. 11:170-175.

Kleiber, M. 1961. *The Fire of Life: An Introduction to Animal Energetics*. New York: Wiley.

Knott, C.D. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology*. 19:1061-1079.

Kowalewski, M.M. and Zunino, G.E. 1999. Impact of deforestation on a population of *Alouatta caraya* in northern Argentina. *Folia Primatologica*. 70(3):163-166.

Kraus, C., Heistermann, M., Kappeler, P.M. 1999. Physiological suppression of sexual function of subordinate males. A subtle form of intrasexual competition among male sifakas *(Propithecus verreauxi)*? *Physiology and Behavior*. 66:855-861.

Krebs, C.J. 1999. *Ecological Methodology*. Addison Wesley Longman, editor. Menlo Park, CA.

Krebs, J.R. and Davies, N.B. 1997. *Behavioural Ecology: An Evolutionary Approach*. Massachusetts: Blackwell Science.

Kress, W.J., Schatz, G.E., Andrianifahanana, M., Morland, H.S. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: Evidence

for an archaic coevolutionary system? *American Journal of Botany*. 81(5):542-551.

Kuntz, R., Kubalek, C., Ruf, T., Tataruch, F., Arnold, W. 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse *(Equus ferus przewalskii)*. *The Journal of Experimental Biology*. 209:4557-4565.

Kurland J.A., and Pearson J.D. 1986. Ecological significance of hypometabolism in nonhuman primates: Allometry, adaptation, and deviant diets. *American Journal of Physical Anthropology*. 71:445–457.

Kuznetsov, V.A., Tchabovsky, A.V., Kolosova, I.E., Moshkin, M.P. 2004. Effect of habitat type and population density on the stress level of Midday Gerbils (*Meriones meridianus* Pall.) in free-living populations. *Biology Bulletin*. 31(6):628-632.

Lack, D. 1950. The breeding seasons of European birds. *Ibis*. 92:288-316.

Lancaster, J.B. and Lee, R.B. 1965. The annual reproductive cycle in monkeys and apes. In: I. DeVore, editor. *Primate Behavior: Field Studies of Monkeys and Apes*. New York: Holt, Rinehart and Winston.

Lane, J. 2006. Can non-invasive glucocorticoid measures be used as reliable indicators of stress in animals? *Animal Welfare*. 15(4):331-342.

Laudenslager, M.L., Ryan, S.M., Drugan, R.C., Hyson, R.L., Maier, S.F. 1983. Coping and immunosuppression: Inescapable but not escapable shock suppresses lymphocyte proliferation. *Science*. 221:568-570.

Le Maho, Y., Goffart, M., Rochas, A., Felabel, H., Chatonnet, J. 1981. Thermoregulation in the only nocturnal simian: the night monkey *Aotus trivirgatus*. *American Journal of Physiology*. 240:R156-R165.

Lee, A.K. and Cockburn, A. 1985. *Evolutionary Ecology of Marsupials*. Cambridge: Cambridge University Press.

Leigh, E.G., Jr. 1999. *Tropical Forest Ecology: a View from Barro Colorado Island*. New York: Oxford University Press.

Leighton, M. and Leighton, D.R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick, editors. *Tropical Rain Forest: Ecology and Management*. Oxford: Blackwell. Pp. 181-196.

Lewis, R.J. and Kappeler, P.M. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*. 67(3):347-364.

Lichtenbelt, W.D.V. 1993. Optimal foraging of a herbivorous lizard, the Green Iguana in a seasonal environment. *Oecologia*. 95(2):246-256.

Lindburg, D.G. 1987. Seasonality of reproduction in primates. In: G. Mitchell and J. Erwin, editors. *Comparative primate biology Vol 2B Behavior, cognition and motivation*. New York: Alan R. Liss. Pp. 167–218.

Lindner, H.R. 1972. Enterohepatic circulation and patterns of urinary excretion of cortisol metabolites in the ewe. *Journal of Endocrinology*. 52:19-20.

Lucas, J.R., Freeberg, T.M., Egbert, J., Schwabl, H. 2006. Fecal corticosterone, body mass, and caching rates of Carolina chickadees *(Poecile carolinensis)* from disturbed and undisturbed sites. *Hormones and Behavior*:634-643.

Lyman, C.P., Willis, S.S., Malan, A., Wang, L.C.H. 1982. *Hibernation and Torpor in Mammals and Birds*. London: Academic Press.

Lynch, J.W., Ziegler, T.E., Strier, K.B. 2002. Individual and seasonal variation in fecal testosterone and cortisol levels of wild male Tufted Capuchin monkeys, *Cebus apella nigritus*. *Hormones and Behavior*. 41:275-287.

MacArthur, R.H. and Pianka, E.R. 1966. On the optimal use of a patchy environment. *American Naturalist*. 100(916):603-609.

MacPhee, R.D.E. and Burney, D.A. 1991. Dating of modified femora of extinct dwarf hippopotamus from southern Madagascar: Implications for constraining human colonialism and vertebrate extinction events. *Journal of Archaeological Science*. 18:695-706.

Magurran, A.E. and Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*. 422(6933):714-716.

Marín, C., Honess, P., Ramíreza, M.J. 2006. Physiological and behavioural study after translocation of a breeding colony of Rhesus Macaques *(Macaca mulatta)*. *Folia Primatologica*. 77(4):319-320.

Marsh, C.W., Johns, A.D., Ayres, J.M. 1987. Effects of habitat disturbance on rain forest primates. In: C.W. Marsh and R.A. Mittermeier, editors. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 83-107.

Martin, R.D. 1972. A preliminary field-study of the Lesser Mouse Lemur *(Microcebus murinus* J. F. Miller 1977). In: P. Charles Dominique and R.D. Martin, editors. *Behaviour and Ecology of Nocturnal Prosimians*. Berlin: Paul Parey. Pp. 43-89.

Martínez-Mota, R., Valdespino, C., Sánchez-Ramos, M.A., Serio-Silva, J.C. 2007. Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Animal Conservation*. 10:374-379.

Mashburn, K.L. and Atkinson, S. 2004. Evaluation of adrenal function in serum and feces of Steller sea lions *(Eumetopias jubatus)*: influences of molt, gender, sample storage, and age on glucocorticoid metabolism. *General and Comparative Endocrinology*. 136(3):371-381.

Mateo, J.M. and Cavigelli, S.A. 2005. A validation of extraction methods for noninvasive sampling of glucocorticoids in free-living ground squirrels. *Physiological and Biochemical Zoology*. 78(6):1069-1084.

May, R.M. and Rubenstein, D.I. 1985. Reproductive strategies. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals: Reproductive Fitness, Book 4*. New York: Cambridge University Press. Pp. 1-23.

McCallister, J.M., Smith, T.E., Elwood, R.W. 2004. Validation of urinary cortisol as an indicator of hypothalamic-pituitary-adrenal function in the bearded emperor tamarin (*Saguinus imperator subgrisescens*). *American Journal of Primatology*. 63(1):17-23.

McEwen, B.S. and Wingfield, J.C. 2003a. The concept of allostasis in biology and biomedicine. *Hormones and Behavior*. 43(1):2-15.

McEwen, B.S. and Wingfield, J.C. 2003b. Response to commentaries on the concept of allostasis. *Hormones and Behavior*. 43(1):28-30.

McKenzie, S. and Deane, E.M. 2005. Faecal corticosteroid levels as an indicator of well-being in the tammar wallaby, *Macropus eugenii*. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology*. 140(1):81-87.

McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist*. 116:106-124.

Mendoza, S.P. and Mason, W.A. 1988. Behavioral and endocrine consequences of heterosexual pair formation in squirrel monkeys. *Physiology and Behavior*. 46:597-603.

Mendoza, S.P. and Mason, W.A. 1991. Breeding readiness in squirrel monkeys: female-primed females are triggered by males. *Physiology and Behavior*. 49(3):471-479.

Merenlender, A., Kremen, C., Rakotondratsima, M., Weiss, A. 1998. Monitoring impacts of natural resource extraction on lemurs of the Masoala Peninsula, Madagascar. *Conservation Ecology* 2(2):5-29.

Merenlender, A.M. 1993. *The Effects of Sociality on the Demogrpahy and Genetic Structure of* Lemur fulvus rufus *(Polygamous) and* Lemur rubriventer *(Monogamous) and the Conservation Implications* [Doctoral Dissertation]. Rochester, New York: University of Rochester.

Meyers, D.M. and Wright, P.C. 1993. Resource tracking: Food availability and *Propithecus* seasonal production. In: P.M. Kappler and Ganzhorn J.U., editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 179-192.

Miller, L.E. 2002. *Eat or be Eaten: Predator Sensitive Foraging among Primates*. New York: Cambridge University Press.

Miller, M.W., Hobbs, N.T., Sousa, M.C. 1991. Detecting stress responses in Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*): Reliability of cortisol concentrations in urine and feces. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 69(1):15-24.

Millspaugh, J.J. and Washburn, B.E. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *General and Comparative Endocrinology*. 138(3):189-199.

Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Washington, DC: Smithsonian Institution Press. Pp. 273-289.

Milton, K. 1984. Habitat, diet, and activity patterns of free-ranging woolly spider monkeys *(Brachyteles arachnoides:* E. Geoffroy 1806). *International Journal of Primatology*. 5(5):491-514.

Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersall, I., Meyers, D.M. 2006. *Lemurs of Madagascar. 2nd Edition*. Washington, DC: Conservation International.

Monfort, S.L., Wasser, S.K., Mashburn, K.L., Burke, M., Brewer, B.A., Creel, S.R. 1997. Steroid metabolism and validation of noninvasive endocrine monitoring in the African wild dog *(Lycaon pictus)*. *Zoo Biology*. 16(6):533-548.

Moore, I.T. and Jessop, T.S. 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Hormones and Behavior*. 43(1):39-47.

Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., Zipparro, V.B. 2000. Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*. 32(4b):811-823.

Morland, H.S. 1991. Preliminary report on the social organization of ruffed lemurs *(Varecia variegata variegata)* in a northeast Madagascar rainforest. *Folia Primatologica*. 56:157-161.

Morland, H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 193-203.

Morton, D.J., Anderson, E., Foggin, C.M., Kock, M.D., Tiran, E.P. 1995. Plasma cortisol as an indicator of stress due to capture and translocation in wildlife species. *Veterinary Record*. 136(3):60-63.

Morton, E.S. 1977. Intratropical migration in the Yellow-green Vireo and Piratic Flycather. *The Auk*. 94:97-106.

Möstl, E., Maggs, J.L., Schrotter, G., Besenfelder, U., Palme, R. 2002. Measurement of cortisol metabolites in faeces of ruminants. *Veterinary Research Communications*. 26(2):127-139.

Möstl, E. and Palme, R. 2002. Hormones as indicators of stress. *Domestic Animal Endocrinology*. 23(1-2):67-74.

Mourão, G. and Medri, Í.M. 2007. Activity of a specialized insectivorous mammal *(Myrmecophaga tridactyla)* in the Pantanal of Brazil. *Journal of Zoology*. 271:187-192.

Muehlenbein, M.P. 2006. Intestinal parasite infections and fecal steroid levels in wild chimpanzees. *American Journal of Physical Anthropology*. 130:546-550.

Müller, M.N. and Wrangham, R. 2004. Dominance, cortisol and stress in wild chimpanzees *(Pan troglodytes schweinfurthii)*. *Behavioral Ecology and Sociobiology*. 55:332-340.

Müllner, A., Linsenmair, K.E., Wikelski, M. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (Opisthocomus hoazin). *Biological Conservation*. 118(4):549-558.

Mutschler, T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur *(Hapalemur griseus alaotrensis)*. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Press. Pp. 221–239.

Nash, L.T. 1998. Vertical clingers and sleepers 1 : Seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*. 69(S1):204-217.

Nash, L.T. 1999. Factors influencing census results on *Lepilemur* and *Microcebus* in southwestern Madagascar. *American Journal of Physical Anthropology*. S28:209.

Negus, N.C. and Berger, P.J. 1972. Environmental factors and reproductive processes in mammalian populations. In: J.T. Velardo and B.A. Kasprow, editors. *Biology of*

Reproduction: Basic and Clinical Studies; *Third Pan American Congress on Anatomy*, New Orleans. Pan American Association of Anatomy: Pp. 89-98.

Negus, N.C. and Berger, P.J. 1987. Mammalian reproductive physiology: Adaptive responses to changing environments. *Current Mammalogy, Volume 1*. New York: Plenum Press. Pp. 149-173.

Nelson, R. and Horning, N. 1993. AVHRR-LAC estimates of forest area in Madagascar, 1990. *International Journal of Remote Sensing*. 14:1463-1475.

Nelson, R.J., Demas, G.E., Klein, S.L., Kriegsfeld, L.J. 2002. *Seasonal Patterns of Stress, Immune Function, and Disease*. New York: Cambridge University Press.

Nelson, R.J. and Klein, S.L. 1999. Environmental and social influences on seasonal breeding and immune function. In: K. Wallen and J.E. Schneider, editors. *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior*. Cambridge: MIT Press Pp. 219-256.

Neville, M.K., Glander, K.E., Braza, F., Rylands, A.B. 1988. The howling monkeys, Genus *Alouatta*. In: R.A. Mittermeier, Rylands, A.B., Coimbra-Filho, A.F., de Fonesco, G.A.B., editor. *Ecology and Behavior of Neotropical Primates*: World Wildlife Fund. Pp. 349-454.

Nicoll, M.E. 2003. *Tenrec ecaudatus,* Tenrec, *Tandraka, Trandraka*. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1283-1287.

Nielsen, E.T. 1983. Relation of behavioural activity rhythms to the changes of day and night. A revision of views. *Behavioural Processes*. 89:147–173.

Nilsson, L.A., Rabakonandrianina, E., Pettersson, B., Gruenmeier, R. 1993. Lemur pollination in the Malagasy rainforest liana *Strongylodon craveniae* (Leguminosae). *Evolutionary Trends in Plants*. 7(2):49-56.

Nisbet, I.C.T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds*. 23:312–332.

Norris, D.O., Donahue, S., Dores, R.M., Lee, J.K., Maldonado, T.A., Ruth, T., Woodling, J.D. 1999. Impaired adrenocortical response to stress by brown trout, *Salmo trutta*, living in metal-contaminated waters of the Eagle River, Colorado. *General and Comparative Endocrinology*. 113(1):1-8.

Norscia I., Carrai V., Borgognini-Tarli S.M. 2006. Influence of dry season and food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. *International Journal of Primatology*. 27:1001-1022.

Nunes, S., Fite, J.E., Patera, K.J., French, J.A. 2001. Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets *(Callithrix kuhli)*. *Hormones and Behavior*. 39:70-82.

Oates, J. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*. 21:1-9.

Oates, J.F. 1977. The guereza and its food. In: T.H. Clutton-Brock, editor. *Primate Ecology*. London: Academic Press. Pp. 276-319.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L., Mole, S. 1990. Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology*. 71(1):328-343.

Onderdonk, D.A. and Chapman, C.A. 2000. Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology*. 21(4):587-611.

Ostner, J., Kappeler, P.M., M., H. 2002. Seasonal variation and social correlates of androgen excretion in male redfronted lemurs *(Eulemur fulvus rufus)*. *Behavioral Ecology and Sociobiology*. 52:485-495.

Overdorff, D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *American Journal of Primatology*. 16(2):143-153.

Overdorff, D., Merelender, AM, Talata, P, Telo, A, Forward, AZ. 1999. Life history of *Eulemur fulvus rufus* from 1988-1997: Implications for ecological stress in southeastern Madagascar. *American Journal of Physical Anthropology* 108:295-310.

Overdorff, D.J. 1992. Differential patterns in flower feeding by *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. *American Journal of Primatology*. 28:191-203.

Overdorff, D.J. 1993b. Ecological and reproductive correlates to range use in red-bellied lemurs *(Eulemur rubriventer)* and rufous lemurs *(Eulemur fulvus rufus)*. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 167-178.

Overdorff, D.J. 1996a. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*. 40(4):327-342.

Overdorff, D.J. 1996b. Ecological correlates to social structure in two Lemur species in Madagascar. *American Journal of Physical Anthropology*. 100(4):487-506.

Overdorff, D.J. 1991. *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufous *and* Eulemur rubriventer *in Madagascar* [Doctoral Dissertation]. Durham: Duke University. 313 p.

Overdorff, D.J., Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Overdorff, D.J. 1993a. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana-National-Park, Madagascar. *International Journal of Primatology*. 14(5):721-753.

Overdorff, D.J., Tecot, S. R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 235-245.

Overdorff, D.J. and Johnson, S. 2003. *Eulemur*, true lemurs. . In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1320-1324.

Overdorff, D.J., Merenlender, A.M., Talata, P., Telo, A., Forward, Z.A. 1999. Life history of *Eulemur fulvus rufus* from 1988-1998 in southeastern Madagascar. *American Journal of Physical Anthropology*. 108:295-310.

Overdorff, D.J. and Rasmussen, M.A. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 61-74.

Overdorff, D.J. and Strait, S.G. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *American Journal of Primatology*. 45:69-82.

Overdorff, D.J. and Tecot, S.R. 2006. Social Pair-bonding and resource defense in wild red-bellied lemurs *(Eulemur rubriventer)*. In: L. Gould and M. L. Sauther, editors. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 235-245.

Palme, R., Robia, C., Messmann, S., Hofer, J., Möstl, E. 1999. Measurement of faecal cortisol metabolites in ruminants: a non-invasive parameter of adrenocortical function. *Wiener Tierarztliche Monatsschrift*. 86(7):237-241.

Passamini, M. 1998. Activity budget of Geoffroy's Marmoset *(Callithrix geoffroyi)* in an Atlantic forest in Southeastern Brazil. *American Journal of Primatology*. 46:333-340.

Paterson, A.M. and Pearce, G.P. 1992. Growth response to humans and corticosteroids in male pigs housed individually and subjected to pleasant, unpleasant or minimal handling during rearing. *Applied Animal Behavior Science*. 34:315-328.

Peel, A.J., Vogelnest, L., Finnigan, M., Grossfeldt, L., O'Brien, J.K. 2005. Non-invasive fecal hormone analysis and behavioral observations for monitoring stress responses in captive western lowland gorillas *(Gorilla gorilla gorilla)*. *Zoo Biology*. 24(5):431-445.

Pereira, M. 1993. Seasonal adustment of growth rate and adult body weight in ringtailed lemurs. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 205-221.

Pereira, M.E., Kaufman, R., Kappeler, P.M., Overdorff, D.J. 1990. Female dominance does not characterize all of the Lemuridae. *Folia Primatologica*. 55:96-103.

Pereira, M.E. 1993. Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: P.M. Kappeler and J.U. Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum Press. Pp. 205-221.

Pereira, M.E. and Kappeler, P.M. 1997. Divergent systems of agonistic behavior in Lemurid primates. *Behaviour*. 134:225–274.

Pereira, M.E., Russ, A.S., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. In: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn and S.M. Goodman, editors. *New Directions in Lemur Studies*. New York: Plenum Publishers.

Pereira, M.E., Strohecker, R.A., Cavigelli, S.A., Hughes, C.L., Pearson, D.D. 1999. Metabolic strategy and social behavior in Lemuridae. *New Directions in Lemur Studies*. New York: Kluwer Acad/Plenum. Pp. 93-118.

Peres, C.A. 1994. Primate responses to phenological changes in an Amazonian terre firme forest. *Biotropica*. 26(1):98-112.

Perret, M. and Predine, J. 1984. Effects of long-term grouping on serum cortisol levels in *Microcebus murinus* Prosimii. *Hormones and Behavior*. 18(3):346-358.

Peters, J. 1999. Understanding Conflicts between People and Parks at Ranomafana, Madagascar. *Agriculture and Human Values*. 16(1):65-74.

Petter, J.J. 1978. Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variations in food production. In: D.J. Chivers and J. Herbert, editors. *Recent Advances in Primatology, vol 1*. New York, NY: Academic Press. Pp. 211-223.

Petter-Rousseaux, A. 1980. Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In: P. Charles-Dominique, Cooper, H.M., Hladik, A., Hladik, C.M., Pages, E., Pariente, G.F., Petter-Rousseaux, A., Petter, J.-J., Schilling, A., editor.

Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior. New York: Academic. Pp. 137-152.

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A., Vasquez, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Association of Science*. 91(7):2805-2809.

Pianka, E. 1994. *Evolutionary Ecology, 5th edition*. New York, NY: Harper Collins.

Pochron, S.T. 2000. Sun avoidance in the yellow baboons *(Papio cynocephalus cynocephalus)* of Ruaha National Park, Tanzania. Variations with season, behaviour and weather. *International Journal of Biometeorology*. 44:141–147.

Pochron, S.T., Tucker, W.T., Wright, P.C. 2004. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986-2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. 125:61-72.

Pollack, J.I. 1979. Spatial distribution and ranging behavior in lemurs. In: G.A. Doyle and R.D. Martin, editors. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 359–409.

Porter, L.M. 1998. Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. *Folia Primatologica*. 69(3):172-176.

Post, E. 2003. Timing of reproduction in large mammals. In: M. D. Schwartz, editor. *Phenology: An Integrative Environmental Science*. Dordecht: Kluwer Academic. Pp. 437-449.

Poulsen, J.R., Clark, C.J., Smith, T.B. 2001. Seasonal variation in the feeding ecology of the grey-cheeked mangabey (*Lophocebus albigena*) in Cameroon. *American Journal of Primatology*. 54:91-105.

Powzyk, J.A. 1997. *The Socio-ecology of Two Sympatric Indriids:* Propithecus diadema diadema *and* Indri indri*, a Comparison of Feeding Strategies and Their Possible Repercussions on Species-Specific Behaviors* [Doctoral Dissertation]. Durham, NC: Duke University.

Prance, G.T. 1980. A note on the probable pollination of *Combretum* by *Cebus* monkeys. *Biotropica*. 12:239.

Pride, E. 2005b. High faecal glucocorticoid levels predict mortality in ring-tailed lemurs *(Lemur catta)*. *Biological Letters*. 1:60-63.

Pride, E. 2005a. Optimal group size and seasonal stress in ring-tailed lemurs *(Lemur catta)*. *Behavioral Ecology*. 16(3):550-560.

Purvis, A. and Hector, A. 2000. Getting the measure of biodiversity. *Nature*. 405(6783):212-219.

Raju, A.J.S. and Rao, S.P. 2006. Pollination by bees and passerine birds and seed dispersal by monkeys in the white teak *Gmelina arborea* Roxb., a commercially important timber tree species in the Eastern Ghats. *Current Science*. 90(2):232-236.

Rasamimanana, H.R. and Rafidinarivo, E. 1993. Feeding behavior of *Lemur catta* females in relation to their physiological state. *Lemur Social Systems and Their Ecological Basis*. New York: Plenum Press. Pp. 123-133.

Raselimanana, A.P. 2003. Gerrhosauridae, Plated Lizards. In: S. M. and Benstead Goodman, J., editor. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 978-983.

Rasmussen, D. 1985. A comparative study of breeding seasonality and litter size in eleven taxa of captive lemurs *(Lemur* and *Varecia)*. *International Journal of Primatology*. 6(5):501-517.

Rasmussen, M.A. 1999. *Ecological Influences on Activity Cycle in Two Cathemeral Primates, the Mongoose Lemur* (Eulemur mongoz) *and the Common Brown Lemur* (Eulemur fulvus fulvus). [Doctoral Dissertation]. Durham, North Carolina: Duke University.

Ratsimbazafy, J. 2002. *On the Brink of Extinction and the Process of Recovery: Responses of Black-and-White Ruffed Lemurs* (Varecia variegata variegata) *to Disturbance in Manombo Forest, Madagascar.* [Doctoral Dissertation]. Stony Brook, NY: State University New York at Stony Brook.

Ratsimbazafy, J. 2006. Diet composition, foraging, and feeding behavior in relation to habitat disturbance: Implications for the adaptability of ruffed lemurs *(Varecia v. editorium)* in Manombo Forest, Madagascar. In: L. Gould and M.L. Sauther, editors. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 403-422.

Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B., Cunningham, E.J.A. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society B*. 273:2713-2719.

Reeder, D.M. and Kramer, K.M. 2005. Stress in free-ranging mammals: Integrating physiology, ecology, and natural history. *Journal of Mammalogy*. 86(2):225-235.

Remaharitra, T. 2006. The effects of anthropogenic disturbances on the structure and composition of rain forest vegetation. *Tropical Resources Bulletin*. 25:32-37.

Rennolls, K. and Laumonier, Y. 2000. Species diversity structure analysis at two sites in the tropical rain forest of Sumatra. *Journal of Tropical Ecology*. 16:253-270.

Rich, E.L. and Romero, L.M. 2005. Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology*. 288(6):R1628-R1636.

Richard, A.F. 1978. Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi:* Lemuriformes. In: G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Washington, D.C.: Smithsonian Institute Press. Pp. 519-533.

Richard, A.F., Sussman, R. W. 1987. Framework for primate conservation in Madagascar. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 329-341.

Richard, A.F. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Richard, A.F. and Dewar, R.E. 1991. Lemur ecology. *Annual Review of Ecology and Systematics* 22:145–175.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*. 39(4):381-391.

Richard, A.F., Dewar, R.E., Schwartz, M., Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *(Propithecus verreauxi verreauxi)*. *Journal of Zoology, London*. 256:421-436.

Richard, A.F. and Nicoll, M.E. 1987. Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. *American Journal of Primatology*. 12:309-314.

Richard, A.F. and Sussman, R.W. 1987. Framework for primate conservation in Madagascar. *Primate Conservation in the Tropical Rain Forest*. New York: Alan R. Liss. Pp. 329-341.

Richter, H.V. and Cumming, G.S. 2006. Food availability and annual migration of the straw-colored fruit bat *(Eidolon helvum)*. *Journal of Zoology*. 268(1):35-44.

Ricklefs, R.E., Miller, G. L. 2000. *Ecology*. New York: W. H. Freeman and Company.

Riley, E.P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*. 28(1):107-133.

Riley, E.P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alternation. *International Journal of Primatology*. 28(1):107-133.

Risler, L., Wasser, S.K., Sackett, G.P. 1987. Measurement of excreted steroids in *Macaca nemestrina*. *American Journal of Primatology*. 12(1):91-100.

Rodríguez-Luna, E., Domínguez-Domínguez, L.E., Morales-Mávil, J.E., Martínez-Morales, M. 2003. Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island. In: L.K. Marsh, editor. *Primates in Fragments: Ecology and Conservation*. New York: Kluwer Academic/Plenum Publishers. Pp. 229-250.

Rodway, M.S., Montevecchi, W.A., Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic puffins *(Fratercula arctica)*. *Biological Conservation*. 76:311-319.

Romero, L.M. 2004. Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*. 19(5):249-255.

Romero, L.M. and Remage-Healey, L. 2000. Daily and seasonal variation in response to stress in captive starlings *(Sturnus vulgaris)*: Corticosterone. *General and Comparative Endocrinology*. 119(1):52-59.

Romero, L.M. and Wikelski, M. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galapagos marine iguanas. *Biological Conservation*. 108(3):371-374.

Romero, M.L. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*. 128:1-24.

Rose, R.M., Gordon, T., Bernstein, I.S. 1978. Diurnal variation in plasma testosterone and cortisol in rhesus monkeys living in social groups. *Journal of Endocrinology*. 76:67-74.

Rusak, B. 1989. The mammalian circadian system: Models and physiology. *Journal of Biological Rhythms*. 4(2):121-134.

Saboureau, M., Laurent, G., Boissin, J. 1979. Daily and seasonal rhythms of locomotor activity and adrenal function in male hedgehogs *(Erinaceus europaeus)*. *Journal of Interdisciplinary Cycle Research*. 10(4):249-266.

Sadlier, R.M.F.S. 1972. Environmental Effects. In: C. R. Austin and R. V. Short, editors. *Reproduction in Mammals, Book 4: Reproductive Patterns*. Cambridge: Cambridge University Press. Pp. 69-94.

Sagar, R. and Singh, J.S. 2006. Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: implications for conservation. *Environmental Conservation*. 33(3):256-262.

Saltzman, W., Schultz-Darken, N.J., Scheffler, G., Wegner, F.H., Abbott, D.H. 1994. Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*. 56(4):801-810.

Sapolsky, R.M. 1982. The endocrine stress response and social status in the wild baboon. *Hormones and Behavior*. 16:279–292.

Sapolsky, R.M. 1983. Endocrine aspects of social instability in the olive baboon *(Papio anubis)*. *American Journal of Primatology*. 5:365-379.

Sapolsky, R.M. 1985. Stress-induced suppression of testicular function in the wild baboon: Role of glucocorticoids. *Endocrinology*. 116:2273-2278.

Sapolsky, R.M. 1986. Endocrine and behavioral correlates of drought in the wild baboons. *American Journal of Primatology*. 11:217-226.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons In: D. Crews, editor. *Psychobiology of Reproductive Behavior: An Evolutionary Perspective*. Englewood Cliffs, New Jersey: Prentice Hall. Pp. 291-322.

Sapolsky, R.M. 1991. Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*. 16(4):281-293.

Sapolsky, R.M. 1992. Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*. 17:701-709.

Sapolsky, R.M. 1992. *Stress, the Aging Brain, and the Mechanisms of Neuron Death*. Cambridge: MIT Press.

Sapolsky, R.M. 1993. Endocrinology alfresco: Psychoendocrine studies of wild baboons. *Recent Progress in Hormone Research*. 48:437-468.

Sapolsky, R.M. 1994. *Why Zebras Don't Get Ulcers: A Guide to Stress, Stress-Related Diseases, and Coping*. New York: W.H. Freeman.

Sauerwein, H., Müller, U., Brüssel, H., Lutz, W., Möstl, E. 2004. Establishing baseline values of parameters potentially indicative of chronic stress in red deer *(Cervus elaphus)* from different habitats in western Germany. *European Journal of Wildlife Research*. 50:168–172.

Sauther, M.L. 1993. Resource competition in wild populations of ringtailed lemurs *(Lemur catta)*: Implications for female dominance. In: P. M. Kappeler and J. U.

Ganzhorn, editors. *Lemur Social Systems and their Ecological Basis*. New York: Plenum. Pp. 135–152.

Sauther, M.L. 1998. The interplay of phenology and reproduction in ringtailed lemurs: Implications for ringtailed lemur conservation. *Folia Primatologica*. 69:309-320.

Sayre, R.W. 1996. *Ecology of Bighorn Sheep in Relation to Habitat and Oil Development in the Little Missouri Badlands* [Doctoral Dissertation]. Grand Forks, North Dakota: University of North Dakota.

Schapiro, S.J., Bloomsmith, M.A., Kessel, A.L., Shively, C.A. 1993. Effects of enrichment and housing on cortisol response in juvenile rhesus monkeys. *Applied Animal Behaviour Science*. 37(3):251-263.

Schatz, G.E. 2001. *Generic Tree Flora of Madagascar*. Kew: Missouri Botanical Gardens and Royal Botanic Garden.

Schiml, P.A., Mendoza, S.P., Saltzman, W., Lyons, D.M., Mason, W.A. 1996. Seasonality in squirrel monkeys *(Saimiri sciureus)*, social facilitation by females. *Physiology & Behavior*. 60(4):1105-1113.

Schmid, J. 1998. Daily torpor in mouse lemurs, *Microcebus* spp.: Metabolic rate and body temperature. *Folia Primatologica*. 69:394-404.

Schmid, J., Kappeler, P.M. 1998. Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur *(Microcebus murinus)*. *Behavioural Ecology and Sociobiology*. 43:125-132.

Schmid, J. and Ganzhorn, J.U. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. *American Journal of Primatology*. 38:169-174.

Schmid, J. and Stephenson, P.J. 2003. Physiological adaptations of Malagasy mammals: Lemurs and tenrecs compared. In: S.M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1198-1203.

Schoech, S.J., Bowman, R., Bridge, E.S., Boughton, R.K. 2007. Baseline and acute levels of corticosterone in Florida Scrub-Jays *(Aphelocoma coerulescens)*: Effects of food supplementation, suburban habitat, and year. *General and Comparative Endocrinology*. 154(1-3):150-160.

Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*. 2:369-404.

Schulkin, J. 2003. Allostasis: a neural behavioral perspective. *Hormones and Behavior*. 43(1):21-27.

Selye, H. 1950. *Stress*. Montreal: ACTA, Incorporated.

Selye, H. 1956. *The Stress of Life*. New York: McGraw-Hill.

Selye, H. 1980. *Selye's Guide to Stress Research, Vol.1*. New York: Van Nostrand Reinhold Company.

Shannon, C.E. and Weaver, W. 1963. *Mathematical Theory of Communication*. Chicago: University of Illinois Press.

Silver, S.C., Marsh, L.K. 2003. Dietary flexibility, behavioral plasticity, and survival in fragments: lessons from translocated howlers. In: L.K. Marsh, editor. *Primates in Fragments: Ecology in Conservation*. New York: Kluwer Academic/Plenum. Pp. 251-265.

Simpson, E.H. 1949. Measurement of diversity. *Nature*. 163:688.

Singh, L. and Singh, J.S. 1991. Species structure, drymatter dynamics and carbon flux of a dry tropical forest in India. *Annals of Botany*. 68:263-273.

Smith, A.P. and Ganzhorn, J.U. 1996. Convergence and divergence in community structure and dietary adaptations in Australian possums and gliders and Malagasy lemurs. *Australian Journal of Ecology*. 21:31-46.

Smith, T.E. and French, J.A. 1997. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets *(Callithrix kuhli)*. *American Journal of Primatology*. 42:253-267.

Smits, L.J., Zielhuis, G.A., Jongbloet, P.H., Straatman, H. 1998. Seasonal variation in human fecundability. *Human Reproduction*. 13(12):3520-3524.

Snodgrass, J.J., Leonard, W.R., Robertson, M.M.M. 2007. Primate bioenergetics: an evolutionary perspective. *Primate Origins: Adaptations and Evolution*. New York: Springer. Pp. 703-737.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. San Francisco: W.H. Freeman.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*. New York: W. H. Freeman.

Sørg, J.-P., Ganzhorn, J.U., Kappeler, P.M. 2003. Forestry and research in the Kirindy Forest/Centre de Formation Professionnelle Forestiere. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1512-1519.

Sørg, J.-P. and Røhner, U. 1996. Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. *Primate Report*. 46(1):57-80.

Sousa, M., Peregrino, H., Cirne, M., Mota, M. 1999. Reproductive patterns and birth seasonality in a South-American breeding colony of common marmosets, *Callithrix jacchus*. *Primates*. 40(2):327-336.

Sousa, M.B.C. and Ziegler, T.E. 1998. Diurnal variation on the excretion patterns of fecal steroids in common marmoset *(Callithrix jacchus)* females. *American Journal of Primatology*. 46(2):105-117.

Southwood, T.R.E. 1978. *Ecological methods: with particular reference to the study of insect populations*. London: Chapman & Hall.

Spellerberg, I.F. and Fedor, P.J. 2003. A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. *Global Ecology and Biogeography*. 12(3):177-179.

Stavisky, R.C., Brandenberger, D., Hook, M., Russell, E., Kaplan, J., Whitten, P. 2001b. The effect of menstrual cycle phase on cortisol excretion on female cynomolgus monkeys *(Macaca fascicularis)*. *American Journal of Primatology*. 54(S1):39-40.

Stavisky, R.C., Whitten, P.L., Hammett, D.H., Kaplan, J.R. 2001a. Lake pigments facilitate analysis of fecal cortisol and behavior in group-housed macaques. *American Journal of Physical Anthropology*. 116(1):51-58.

Stavisky, R.C., Wilson, M., Russell, E., Whitten, P.L. 1994. Validation of the fecal extraction method: Correlation of serum and fecal endocrine profiles in rhesus macaques, *Macaca mulatta*. *American Journal of Physical Anthropology*. (S18):186.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review in Biology*. 51:3-47.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Stephenson, P.J. 2003. Lipotyphla (ex Insectivora): *Geogale aurita,* Large-eared Tenrec. In: S. M. Goodman and J. Benstead, editors. *The Natural History of Madagascar*. Chicago: University of Chicago Press. Pp. 1265-1273.

Sterling, P. and Eyer, J. 1988. Allostasis: A new paradigm to explain arousal pathology. In: S. Fisher and J. Reason, editors. *Handbook of Life Stress, Cognition and Health*. New York: John Wiley & Sons.

Stoner, K.E. 1996. Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys *(Alouatta palliata)* in northeastern Costa Rica. *International Journal of Primatology*. 17(1):1-30.

Storey, A.E., Walsh, C.J., Quinton, R.L., Wynne-Edwards, K.E. 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution of Human Behavior*. 21:79-95.

Strier, K.B. 1986. *The Behavior and Ecology of the Woolly Spider Monkey, or Muriqui* (Brachyteles arachnoides) [Doctoral Dissertation]. Cambridge, MA: Harvard University.

Strier, K.B. 1987. Activity budgets of Woolly Spider monkeys or Muriquis *(Brachyteles arachnoides)*. *American Journal of Physical Anthropology*. 13:385-195.

Strier, K.B. and Ziegler, T.E. 1997. Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *American Journal of Primatology*. 42(4):299-310.

Strier, K.B. and Ziegler, T.E. 2005. Advances in field-based studies of primate behavioral endocrinology. *American Journal of Primatology*. 67(1):1-4.

Strier, K.B., Ziegler, T.E., Wittwer, D.J. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis *(Brachyteles arachnoides)*. *Hormones and Behavior*. 35:125-134.

Struhsaker, T.T. 1997. *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. Gainseville: University Press of Florida.

Sussman, R.W. 1974. Ecological distinctions in sympatric species of *Lemur*. In: R.D. Martin, G.A. Doyle and A.C. Walker, editors. *Prosimian Biology*. London: Duckworth.

Sussman, R.W., Garber, P.A., Cheverud, J.M. 2005. Importance of cooperation and affiliation in the evolution of primate sociality. *AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY*. 128(1):84-97.

Sussman, R.W. and Raven, P.H. 1978. Pollination by lemurs and marsupials: an archaic evolutionary system. *Science*. 200:731-736.

Swarup, A. 2007. Red Cross -- Red Crescent respond to cyclones in Madagascar. International Federation of Red Cross and Red Crescent Societies (IFRC)--Switzerland.

Tan, C.L. 2000. *Behavior and ecology of three sympatric bamboo lemur species (genus* Hapalemur*) in Ranomafana National Park, Madagascar* [Doctoral Dissertation]. United States -- New York: State University of New York at Stony Brook.

Tarlow, E.M. and Blumstein, D.T. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*. 102(3-4):429-451.

Tarnaud, L. 2006. Cathemerality in the Mayotte Brown Lemur *(Eulemur fulvus)*: Seasonality and food quality. *Folia Primatologica*. 77(1-2):166-177.

Tattersalll, I. 1976. Group structure and activity rhythm in *Lemur mongoz* (Primates, lemuriformes) on Anjouan and Moheli islands, Comoro archipelago. *Anthropological Papers of the American Museum of Natural History*. 53:363–378.

Tattersalll, I. 1987. Cathemeral activity in primates - a definition. *Folia Primatologica*. 49(3-4):200-202.

Tattersalll, I. 2006. The concept of cathemerality: History and definition. *Folia Primatologica*. 77(1-2):7-14.

Taylor, C.R., Heglund, N.C., Maloiy, G.M. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*. 97:1-21.

Tecot, S. 2006. Activity budget and microhabitat in *Eulemur rubriventer*. *American Journal of Primatology*. 68(1):111-112.

Tecot, S. 1999. *The Effect of Habitat on Fecal Cortisol Concentrations in Squirrel Monkeys (Saimiri sciureus)* [Master's Thesis]. Austin: University of Texas at Austin.

Tecot, S. 2007b. Fecal cortisol levels and maintenance behaviors in wild groups of a cooperatively breeding species, the red-bellied lemur *(Eulemur rubriventer)*. *American Journal of Primatology*. 69(1):127.

Tecot, S. 2001. Field methods for collecting fecal cortisol: A test of four Malagasy primates. *American Journal of Primatology*. 54(S1):32-33.

Tecot, S. 2007a. Seasonality, phenology, and feeding by *Eulemur rubriventer* in two sites in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*. S44:230.

Tecot, S. and Overdorff, D. 2005. Aseasonal births and reproductive patterns in *Eulemur rubriventer* in southeastern Madagascar. *American Journal of Primatology*. 66(S1):111-112.

Tecot, S. and Overdorff, D. 2006. The influence of feeding behavior on reproduction in *Eulemur rubriventer* in SE Madagascar. *American Journal of Physical Anthropology*. S42:175.

Terborgh, J. 1986a. Community aspects of frugivory in tropical forests. In: A. Estrada and T.H. Fleming, editors. *Frugivores and Seed Dispersal*. Dordrecht: Dr. W. Junk Publishers. Pp. 372-384.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton, N.J.: Princeton University Press.

Terborgh, J. 1986b. Keystone plant resources in the tropical forest. In: M.E. Soulé, editor. *Conservation Biology, the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates, Inc. Pp. 330–344.

Terio, K.A., Citino, S.B., Brown, J.L. 1999. Fecal cortisol metabolite analysis for noninvasive monitoring of adrenocortical function in the cheetah *(Acinonyx jubatus)*. *Journal of Zoo and Wildlife Medicine*. 30(4):484-491.

Terranova, C.J., Coffman, B.S. 1997. Body weights of wild and captive lemurs. *Zoo Biology*. 16(1):17-30.

Tilden, C.D. and Oftedal, O.T. 1995. The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: L Alterman, GA Doyle and MK Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press. Pp. 119-131.

Torres de Assumpção, C. 1981. *Cebus apella* and *Brachyteles arachnoides* (Cebidae) as potential pollinators of *Mabea fistulifera* (Euphorbiaceae). *Journal of Mammalogy*. 62:386-388.

Touma, C. and Palme, R. 2005. Measuring fecal glucocorticoid metabolites in mammals and birds: The importance of validation. *Annals of the New York Academy of Sciences*. 1046(1):54-74.

Touma, C., Palme, R., Sachser, N. 2004. Analyzing corticosterone metabolites in fecal samples of mice: a noninvasive technique to monitor stress hormones. *Hormones and Behavior*. 45(1):10-22.

Traveset, A. 1999. The importance of mutualisms for biodiversity conservation in insular ecosystems. *Revista Chilena de Historia Natural*. 72(4):527-538.

Tsuji, Y., Fujita, S., Sugiura, H., Saito, C., Takatsuki, S. 2006. Long-term variation in fruiting and the food habits of wild Japanese macaques on Kinkazan Island, northern Japan. *American Journal of Primatology*. 68:1068-1080.

Turk, D. 1995. *A Guide to the Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Turk, D. 1995. *A Guide to Trees of Ranomafana National Park and Central Eastern Madagascar*. Washington, D.C.: USAID.

Turk, D. 1997. *A Guide to Trees of Eastern Madagascar and Ranomafana National Park*. Missouri Botanical Garden, St. Louis.

Turner, I.M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology*. 33(2):200-209.

Ulyan, M.J., Burrows, A.E., Buzzell, C.A., Raghanti, M.A., Marcinkiewicz, J.L., Phillips, K.A. 2006. The effects of predictable and unpredictable feeding schedules on the behavior and physiology of captive brown capuchines *(Cebus apella)*. *Applied Animal Behaviour Science*. 101:154-160.

UNDP. 2006. *World Development Report*. Oxford: United Nations Development Programme.

UNESCO. 2003. *United Nations Educational Scientific and Cultural Organization World Heritage News*.

Vaanholt, L.M., Garland, T., Jr., Daan, S., Visser, G.H. 2007. Wheel-running activity and energy metabolism in relation to ambient temperature in mice selected for high wheel-running activity. *Journal of Comparative Physiology*. 177:109-118.

van Horn, R.N. and Eaton, G.G. 1979. Reproductive physiology and behavior in prosimians. In: R. D. Martin, editor. *The Study of Prosimian Behavior*. New York: Academic Press. Pp. 79-122.

van Schaik, C., and van Noordwijk, MA. 1985. Interannual variability in fruit abundance and reproductive seasonality in Sumatran long-tailed macaques *(Macaca fascicularis)*. *Journal of Zoology*. 206:533-549.

van Schaik, C.P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology*. 2:327-347.

van Schaik, C.P. and Kappeler, P.M. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*. 102:915-941.

van Schaik, C.P. and Pfannes, K.R. 2005. Tropical climates and phenology: a primate perspective. In: D.K. Brockman and C.P. van Schaik, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates*. Cambridge: Cambridge University Press. Pp. 23-54.

van Schaik, C.P., Terborgh, J., Wright, S.J. 1994. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*. 24:353-377.

van Schaik, C.P., Terborgh, J.W., Wright, S.J. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecological Systems*. 24:353-377.

Vasey, N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology*. 112(3):411-431.

Vasey, N. 2004. Circadian rhythms in diet and habitat use in red ruffed lemurs *(Varecia rubra)* and white-fronted brown lemurs *(Eulemur fulvus albifrons)*. *American Journal of Physical Anthropology*. 124(4):353-363.

Vasey, N. 2005. Activity budgets and activity rhythms in red ruffed lemurs *(Varecia rubra)* on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. *American Journal of Primatology*. 66(4):393-394.

von der Ohe, C.G., Wasser, S.K., Hunt, K.E., Servheen, C. 2004. Factors associated with fecal glucocorticoids in Alaskan Brown bears *(Ursus arctos horribilis)*. *Physiological and Biochemical Zoology*. 77(2):313-320.

Waas, J.R., Ingram, J.R., Matthews, L.R. 1999. Real-time physiological responses of red deer to translocations. *Journal of Wildlife Management*. 63(4):1152-1162.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2005. Field endocrinology and conservation biology. *Integrative and Comparative Biology*. 45(1):12-18.

Walker, B.G., Boersma, P.D., Wingfield, J.C. 2006. Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology*. 20(1):146-154.

Walsberg, G.E. 2003. How useful is energy balance as a overall index of stress in animals? *Hormones and Behavior*. 43(1):16-17.

Wang, L.C.H. 1989. Ecological, physiological and biochemical aspects of torpor in mammals and birds. In: L.C.H. Wang, editor. *Advances in Comparative and Environmental Physiology*. Berlin: Springer-Verlag. Pp. 361–401.

Wasser, S.K. 1996. Reproductive control in wild baboons measured by fecal steroids. *Biology of Reproduction*. 55(2):393-399.

Wasser, S.K., Bevis, K., King, G., Hanson, E. 1997. Noninvasive physiological measures of disturbance in the Northern Spotted Owl. *Conservation Biology*. 11(4):1019-1022.

Wasser, S.K., Bevis, K., King, G., Hanson, E. 1997. Non-invasive physiological measures of disturbance in the Northern spotted owl. *Conservation Biology*. 11:1019–1022.

Wasser, S.K., Hunt, K.E., Brown, J.L., Cooper, K., Crockett, C.M., Bechert, U., Millspaugh, J.J., Larson, S., Monfort, S.L. 2000. A generalized fecal

glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *General and Comparative Endocrinology*. 120(3):260-275.

Wasser, S.K. and Starling, A.K. 1988. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology*. 16(2):97-121.

Wasser, S.K., Thomas, R., Nair, P.P., Guidry, C., Southers, J., Lucas, J., Wildt, D.E., Monfort, S.L. 1993. Effects of dietary fiber on faecal steroid measurements. *Journal of Reproduction and Fertility*. 97:569-574.

Watson, S.L., Ward, J.P., Davis, K.B., Stavisky, R.C. 1999. Scent-marking and cortisol response in the small-eared bushbaby *(Otolemur garnettii)*. *Physiology and Behavior*. 66(4):695-699.

Watts, D.P. 1988. Environmental influences on Mountain gorilla time budgets. *American Journal of Primatology*. 15:195-211.

Weathers W.W., and Nagy K.A. 1980. Simultaneous Doubly Labeled Water (3hh18o) and time-budget estimates of daily energy-expenditure in *Phainopepla nitens*. Auk. 97*:*861-867.

Wehr, A. 1998. Effect of seasonal changes in daylength on human neuroendocrine function. *Hormone Research*. 49(3-4):118-124.

Weinberg, C.R., Moledor, E., Baird, D.D. 1994. Is there a seasonal pattern in risk of early-pregnancy loss. *Epidemiology*. 5(5):484-489.

Weingrill, T., Gray, D.A., Barrett, L., Henzi, S.P. 2004. Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. *Hormones and Behavior*. 45(4):259-269.

White, F., Overdorff, D.J., Balko, E., Wright, P.C. 1995. Distribution of ruffed lemurs *(Varecia variegata)* in Ranomafana National Park, Madagascar. *Folia Primatologica*. 64:124-131.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*. 21:213-251.

Whitten, P. 2000. Evolutionary endocrinology of the cercopithecoids. In: P.F. Whitehead and C.J. Jolly, editors. *Old World Monkeys*. Cambridge: Cambridge University Press. Pp. 269-297.

Whitten, P.L. and Brockman, D.K. 2001. Strepsirrhine reproductive ecology. In: P.T. Ellison, editor. *Reproductive Ecology and Human Evolution*. New York: Aldine de Gruyter. Pp. 321-350.

Whitten, P.L., Brockman, D.K., Stavisky, R.C. 1998a. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*. Pp. 1-23.

Whitten, P.L., Stavisky, R., Aureli, F., Russell, E. 1998b. Response of fecal cortisol to stress in captive chimpanzees *(Pan troglodytes)*. *American Journal of Primatology*. 44(1):57-69.

Wiebe, R.H., Williams, L.E., Abee, C.R., Yeoman, R.R., Diamond, E.J. 1988. Seasonal changes in serum dehydroepiandrosterone, androstenedione, and testosterone levels in the squirrel monkey (*Saimiri boliviensis boliviensis*). *American Journal of Primatology*. 14(3):285-291.

Wikelski, M., Hau, M., Wingfield, J.C. 2000. Seasonality of reproduction in a neotropical rain forest bird. *Ecology*. 81(9):2458-2472.

Williamson, M. and Gaston, K.J. 2005. The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. *Journal of Animal Ecology*. 74(3):409-422.

Wilson, M.I., Brown, G.M., Wilson, D. 1978. Annual and diurnal changes in plasma androgen and cortisol in adult male squirrel monkeys *(Saimiri sciureus)* studied longitudinally. *Acta Endocrinologica*. 87(2):424-433.

Wingfield, J.C. 2003. Anniversary Essay: Control of behavioural strategies for capricious environments. *Animal Behaviour*. 66:807-816.

Wingfield, J.C. 2005. Flexibility in annual cycles of birds: implications for endocrine control mechanisms. *Journal of Ornithology*. V146(4):291-304.

Wingfield, J.C., Hunt, K., Breuner, C., Dunlap, K., Fowler, G.S., Freed, L., Lepson, J. 1997. Environmental stress, field endocrinology, and conservation biology. In: JR Clemmons and R Buchholz, editors. *Behavioral Approaches to Conservation in the Wild* Cambridge: Cambridge University Press. Pp. 95-131.

Wingfield, J.C. and Kitaysky, A.S. 2002. Endocrine responses to unpredictable environmetnal events: Stress or anti-stress hormones? *Integrative and Comparative Biology*. 42:600-609.

Wingfield, J.C. and Romero, L.M. 2001. Adrenocortical responses to stress and their modulation in free-living vertebrates. In: B.S. McEwen and H.M. Goodman, editors. *Handbook of Physiology, Section 7: The Endocrine System, VolIV: Coping with the Environment: Neural and Endocrine Mechanisms*. New York: Oxford University Press. Pp. 211-234.

Wingfield, J.C. and Sapolsky, R.M. 2003. Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*. 15(8):711-724.

Wright, P. 2006. Considering climate change effects in lemur ecology and conservation. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 385-401.

Wright, P.C. 1992. Primate ecology, rainforest conservation and economic development: Building a National Park in Madagascar. *Evolutionary Anthropology*. 1:25-33.

Wright, P.C. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*. 16(5):835-854.

Wright, P.C. 1997. The future of biodiversity in Madagascar: A view from Ranomafana National Park. In: S. G. Goodman and B. D. Patterson, editor. *Natural Change and Human Impact in Madagascar*. Washington, D.C.: Smithsonian Institution Press. Pp. 381-405.

Wright, P.C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology*. 42:31-72.

Wright, P.C. 2006. Considering Climate Change Effects in Lemur Ecology and Conservation. In: L. Gould and M.L. Sauther, editor. *Lemurs: Ecology and Adaptation*. New York: Springer. Pp. 385-401.

Wright, P.C. and Andriamihaja, B. 2002. Making a Rain Forest National Park Work in Madagascar: Ranomafana National Park and Its Long-term Research Commitment. In: J. Terborgh, C. van Schaik, L. Davenport and M. Rao, editors. Making Parks Work: Strategies for Preserving Tropical Nature. Washington: Island Press. Pp. 112-136.

Wright, P.C. and Martin, L.B. 1995. Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: L. Alterman, G.A. Doyle and M.K. Izard, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum. Pp. 45-60.

Wright, P.C. and Razafindratsita, T., Pochron, S.T., Jernvall, J. 2005. The key to frugivory in Madagascar. In: J.L. Dew and J.P. Boubli, editors. *Tropical Fruits and Frugivores: The Search for Strong Interactors.* New York: Kluwer Academic/Plenum. Pp. 118-128.

Wright, S.J. and van Schaik, C.P. 1994. Light and the phenology of tropical trees. *American Naturalist*. 143:192-199.

Young, A.L., Richard, A.F., Aiello, L.C. 1990. Female dominance and maternal investment in Strepsirhine primates. *American Naturalist*. 135:473-488.

Young, A.L., Richard, A.F., Aiello, L.C. 1990. Female dominance and maternal investment in Strepsirhine primates. *American Naturalist*. 135:473-488.

Zav'yalov, E.L., Gerlinskaya, L.A., Evsikov, V.L. 2003. Estimation of stress level in the bank vole *Clethrionomys glareolus* (Rodentidae, Rodentia) by fecal corticosterone. *Zoologichesky Zhurnal*. 82(4):508-513.

Ziegler, T.E. 2000. Hormones associated with non-maternal infant care: A review of mammalian and avian studies. *Folia Primatologica*. 71:6-21.

Ziegler, T.E., Scheffler, G., Snowdon, C.T. 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*. 29(3):407-424.

Ziegler, T.E. and Tecot, S. 2007. Cooperative breeding in nonhuman primates: A broader approach. *American Journal of Primatology*. 69(1):126.

Ziegler, T.E., Washabaugh, K.F., Snowdon, C.T. 2004. Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*. 45(2):84-92.

Ziegler, T.E., Wegner, F.H., Snowdon, C.T. 1996. Hormonal responses to parental and nonparental conditions in male cotton-top tamarins, *Saguinus oedipus*, a New World primate. *Hormones and Behavior*. 30(3):287-297.

Ziegler, T.E. and Wittwer, D.J. 2005. Fecal steroid research in the field and laboratory: Improved methods for storage, transport, processing, and analysis. *American Journal of Primatology*. 67(1):159-174.

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